

CARBONIFEROUS SCHIZOPHORIID BRACHIOPODS FROM WESTERN EUROPE

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ABSTRACT. Six species of the genus *Schizophoria* are described from the Carboniferous of western Europe. *Schizophoria annectans* is new. All species are shown to be externally and internally distinct. Stratigraphical ranges and postulated phylogeny are also given.

THE genus *Schizophoria* has been studied from the Carboniferous of Belgium and the British Isles. The precise stratigraphical range and relative abundance of *Schizophoria* from the Dinant Basin of Belgium is unknown, due to absence of extensive collections, and lack of detailed information on horizons. Available information is listed under specific descriptions.

In the British Isles *Schizophoria* has a long stratigraphical and wide geographical range. The genus appears in the K zone, becomes very abundant in the reef facies (C–D zones), and eventually disappears towards the top of the Viséan, except for *S. connivens* (Phillips). *Schizophoria connivens* continues to occur in limestones (E stage) of the Scottish Namurian succession, and marine Cayton Gill Beds (R₁ stage) of the Yorkshire Namurian succession.

Abbreviations. In the descriptions, relevant museum collections listed are as follows: BC—Bedford College, University of London; BM—British Museum (Natural History); GSI—Geological Survey of Ireland (Dublin); GSL—Geological Survey (Leeds); GSM—Geological Survey Museum (London); HMUG—Hunterian Museum, University of Glasgow; IC—Imperial College, University of London; IRSN—Institut royal des sciences naturelles de Belgique; SM—Sedgwick Museum, University of Cambridge; TCD—Trinity College, Dublin; UR—University of Reading.

In each text-figure of serial sections, the numbers represent distances in millimetres measured anteriorly from the umbones. Almost all muscle field patterns and vascular markings are illustrated on figures of internal moulds, since moulds, rather than discrete valves, are the common form of preservation.

SYSTEMATIC DESCRIPTION

Superfamily ENTELETACEA Waagen 1884

Family SCHIZOPHORIIDAE Schuchert and Le Vene 1929

Subfamily SCHIZOPHORIINAE Schuchert and Le Vene 1929

Genus SCHIZOPHORIA King 1850

Schizophoria connivens (Phillips) 1836

Plate 18, figs. 1, 2; text-figs. 1–4

1836 *Spirifera connivens* Phillips, p. 220, pl. 11, fig. 2.

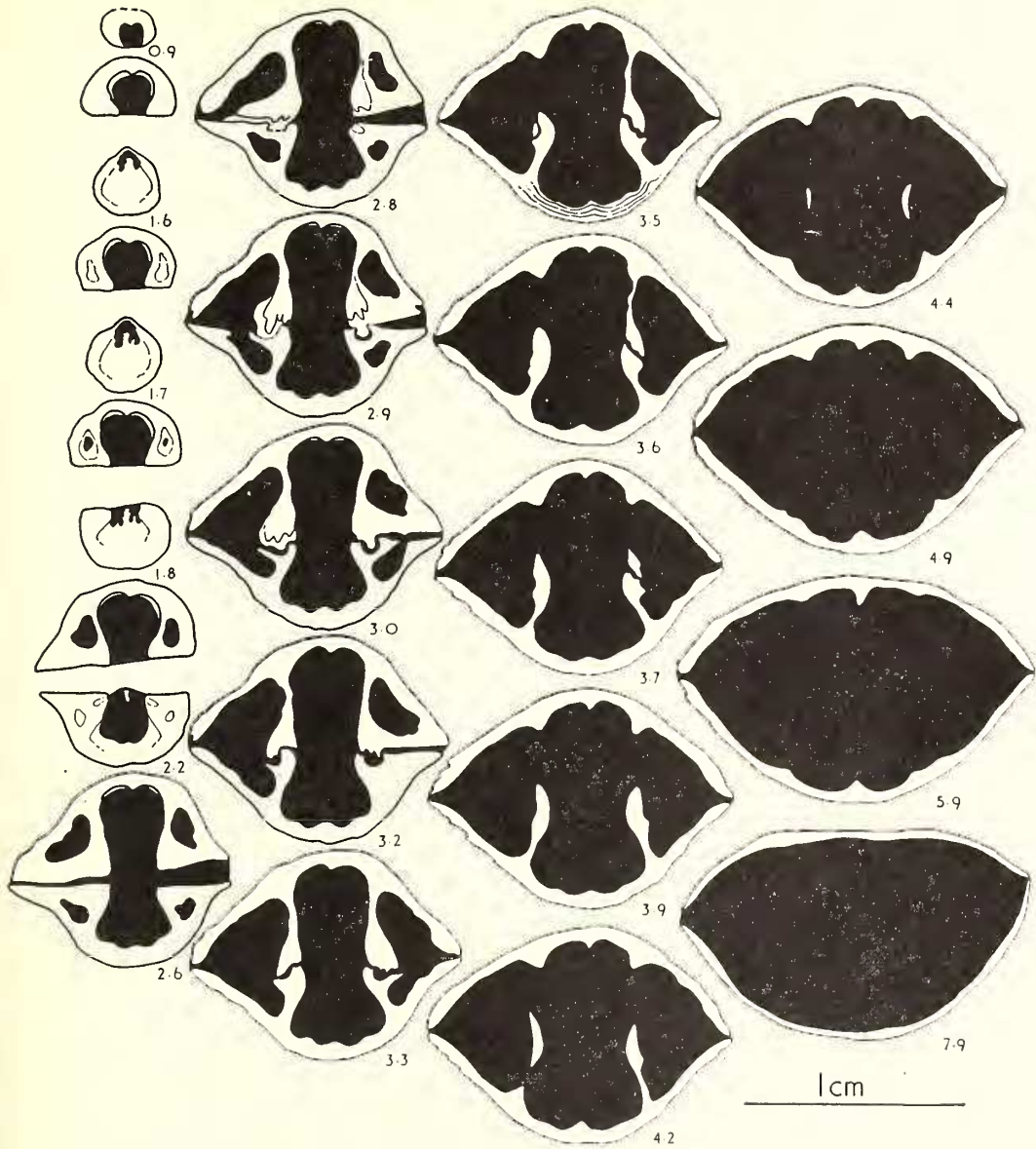
1842–4 *Orthis striatula* De Koninck, p. 224, pl. 13, fig. 11a, b; non pl. 13^{bis}, fig. 6.

1861 *Schizophoria resupinata* var. *connivens* (Phillips); Davidson, p. 131, pl. 29, figs. 6, 7.

1923 *Schizophoria resupinata* var. *connivens* (Phillips); Demanet, p. 121, pl. 5, fig. 3.

1923 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, pl. 5, fig. 2.

1932 *Schizophoria hudsoni* George, p. 38, figs. 51–53.



TEXT-FIG. 1. *Schizophoria connivens* (Phillips). Transverse serial sections (IC 11137); D₁ zone, Swinden, Yorkshire; Length 13.7 mm., width 16.7 mm., depth 11.5 mm.

1934 *Schizophoria resupinata* var. *connivens* (Phillips); Demanet, p. 56, pl. 4, figs. 5, 6.

1941 *Schizophoria connivens* (Phillips); Bond, p. 293, text-fig. 35.

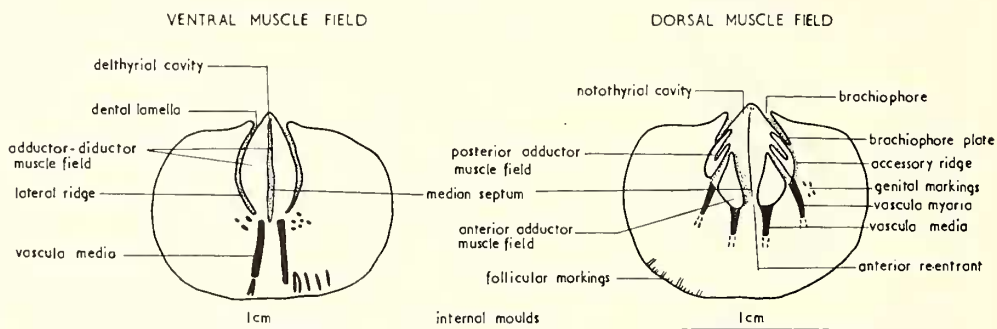
1962 *Schizophoria* aff. *S. resupinata* (Martin); Yanagida, pl. 21, fig. 5.

Type. The holotype is lost. The neotype, chosen and figured by Bond (1941), is deposited in the British Museum (Natural History), B387.

Diagnosis. Small to medium, tumid, rectangular to rounded, with biplicate, sulciphate

or quadrate-uniplicate anterior commissure. Shell coarsely costellate, rugate. Ventral muscle field strongly incised, elliptical to flabellate. Short, strong brachiophore plates.

Description. Shell ventribiconvex to weakly dorsibiconvex, with greatest shell width at or slightly anterior to mid-length. Ventral sulcus ill-defined, originating anterior of umbo, broadening and deepening anteriorly. Dorsal sulcus frequently developed. Anterior commissure varying from biplicate to sulcinate or uniplicate. Costellae coarse, 4 in 1 mm. at 10 mm. from beaks. Scattered costellae thickened, with spine bases developed anteriorly. Prominent growth rugae.



TEXT-FIG. 2. *Schizophoria connivens* (Phillips). Ventral and dorsal muscle fields, based on specimens BC B272, 275; BM B47673, 5709; GSL 2830; UR 13595.

Teeth compound, supported by anteriorly and ventrally divergent dental lamellae (text-fig. 1, sections 2.2–3.3). Articulation supplemented by interlocking ends of brachiophores and dental lamellae. Ventral muscle field (text-fig. 2) one-half valve length, elliptical to flabellate, strongly incised. Median septum varying from narrow to broad, subangular to rounded, broadening and increasing in height anteriorly (text-fig. 1, sections 0.9–5.9). Two slightly divergent vascula media (text-fig. 2).

Myophore compound, average width 1.5 mm., with central ridge bordered by two lateral ridges. Stubby brachiophores fused to strong, short, divergent brachiophore plates (text-fig. 1, sections 2.6–4.2). Dental sockets articulating with ventral teeth (text-fig. 1, sections 2.8–3.3). Dorsal muscle field (text-fig. 2) moderately incised, elliptical to rounded, one-half to two-thirds valve length. Accessory ridges reflexed anteriorly to form shallow, subangular re-entrant. Median septum subrounded, broadening and increasing in height, and becoming sharp crested anteriorly (text-fig. 1, sections

EXPLANATION OF PLATE 18

Figs. 1, 2. *Schizophoria connivens* (Phillips). 1, Ventral view, BC B146 ($\times 2$). 2, Anterior view, SM D.22.B ($\times 2$).

Fig. 3. *Schizophoria gibbera* (Portlock). 3a, b, Dorsal and anterior views, holotype, GSM 70646 ($\times 1\frac{1}{2}$).

Figs. 4, 5. *Schizophoria linguata* (Quenstedt). 4a, Lateral view, type specimen, Tübingen 55,152 ($\times 2$).

5a, b, Ventral and anterior views, type specimen, Tübingen 55,153 ($\times 2$).

Fig. 6. *Schizophoria annectans* sp. nov. 6a, b, c, Ventral, anterior and lateral views, holotype, BM B40126 ($\times 2$).

Fig. 7. *Schizophoria resupinata* (Martin). 7a, b, Dorsal and anterior views, BC B175 ($\times 1\frac{1}{2}$).

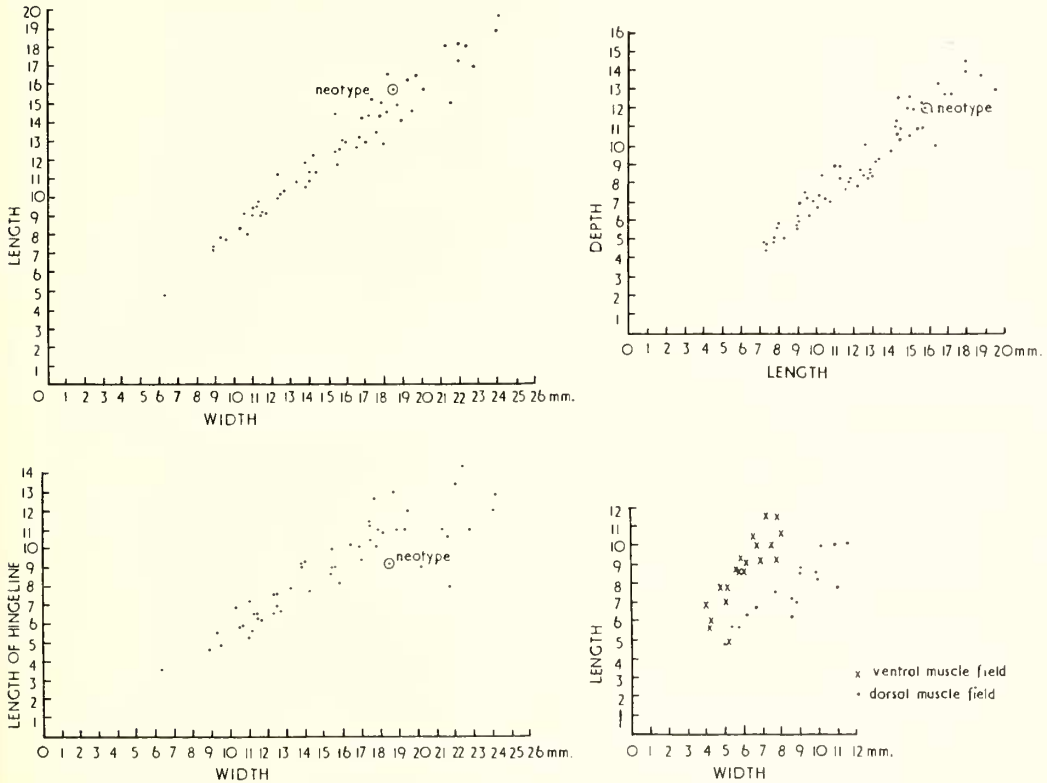
Fig. 8. *Schizophoria woodi* Bond. 8a, b, Dorsal and lateral views, BM B54121 ($\times 1\frac{1}{2}$).



2.6–5.9). Anterior adductor muscle scar pyriform; posterior muscle scar digitate. Two vascula media, two vascula myaria (text-fig. 2). Genital markings developed postero-laterally. Follicular markings occasionally developed peripherally on internal moulds.

Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 3.

S. CONNIVENS (PHILLIPS)



TEXT-FIG. 3. Dimensions of *Schizophoria connivens* (Phillips).

Remarks. *Schizophoria connivens* superficially resembles small, rugate forms of *S. resupinata* (Martin), but is distinguished externally by its more tumid outline, biplicate or quadrate-uniplicate anterior commissure, and coarser costellae. Internally, the elliptical to flabellate ventral muscle field, short, stout brachiophore plates of *S. connivens* contrast with the more flabellate ventral muscle field, and longer, more slender brachiophore plates of *S. resupinata*.

Schizophoria connivens also superficially resembles older, rugate specimens of *S. woodi* Bond from Treak Cliff, in size, outline, and prominent rugae. But *S. connivens* has coarse costellae, and a biplication or quadrate-uniplication, in contrast to the finer costellae and angular-uniplication of *S. woodi*.

Comparisons with other species are given on text-fig. 4.

	SIZE	OUTLINE	CONVEXITY	ANTERIOR COMMISSURE	ORNAMENT	DENTAL LAMELLAE	VENTRAL MUSCLE FIELD	BRACHIOPHORES BRACHIOPHORE PLATES	DORSAL MUSCLE FIELD
SCHIZOPHORIA RESUPINATA (MARTIN)	medium large	rectangular elliptical	ventribiconvex biconvex moderately dorsibiconvex	rectimarginate uniplicate unisulcate subplicate	costellae fine some thick costellae with spine bases rugae weak absent	ventrally subparallel	broad labellate moderately incised	stubby brachiophores slender divergent brachiophore plates	elliptical moderately incised
SCHIZOPHORIA CONNIVENS (PHILLIPS)	medium small	rectangular rounded	ventribiconvex biconvex moderately dorsibiconvex	quadrate uniplicate biplicate subplicate	costellae coarse with spine bases rugae prominent	ventrally subparallel divergent	moderately narrow oval	stubby brachiophores stout divergent brachiophore plates	elliptical rounded moderately incised
SCHIZOPHORIA GIBBERA (PORTLOCK)	medium large	elliptical rounded	strongly dorsibiconvex	rounded uniplicate	costellae very fine some thick costellae rugae present	ventrally convergent	narrow parallel- sided incised	stubby brachiophores long slender curved brachiophore plates	rectangular elliptical strongly incised
SCHIZOPHORIA LINGUATA (QUENSTEDT)	medium small	rectangular elliptical	great ontogenetic in dorsibiconvexity	rounded uniplicate	costellae very fine some thick costellae rugae present	ventrally subparallel	narrow parallel- sided incised	stubby brachiophores long slender curved brachiophore plates	rectangular elliptical moderately incised
SCHIZOPHORIA ANNECTANS N. SP.	medium small	rectangular elliptical	biconvex moderately dorsibiconvex	rounded uniplicate	costellae very fine some thick costellae rugae prominent	ventrally subparallel	narrow parallel- sided incised	stubby brachiophores long curved brachiophore plates	rectangular elliptical moderately incised
SCHIZOPHORIA WOODI BOND	large small	rounded rectangular elliptical	strongly dorsibiconvex	angular uniplicate	costellae very fine some thick costellae with spine bases rugae prominent	ventrally subparallel	broad labellate strongly incised	stubby brachiophores long slender curved brachiophore plates	labellate moderately incised

TEXT-FIG. 4. Comparisons of Carboniferous species of *Schizophoria*.

Although *S. connivens* is a long ranging species, there is apparently little external and internal variation between early and late forms.

Schizophoria hudsoni George is listed in synonymy with *S. connivens*. *S. hudsoni* from the Cayton Gill Beds of the Millstone Grit are preserved as external and internal moulds. But these moulds resemble *S. connivens* in outline, anterior plication, coarsely costellate and rugate shell, and form of the muscle fields.

Material. Belgium, Visé: Viséan (IRSN 2737). Derbyshire: *Dielasma* Bed, D₁, Treak Cliff, Castleton (BC B137, 138); Carboniferous Limestone, Longnor (BM B34460); Carboniferous Limestone, D₂, Park Hill, Longnor (GSM 34243, 34247, 84682, 84686). Isle of Man (Castletown): Carboniferous Limestone, D₂, Poolvash (HMUG L53461, 2, 5). Ireland: Lower Carboniferous, C₁₋₂, Millicent, Kildare (BM B13184); C₁₋₂ subzones, Ballylin, Limerick (UR 13593, 13595); Viséan, D₁, Meath (TCD 3593-8). Lancashire: Carboniferous Limestone, Clitheroe (SM E6502, 6505, 6506). Scotland: Carboniferous Limestone, D₃, Corrie Burn, Campsie (HMUG L131/2, 3; L4272/2, 3; L5343/1); Carboniferous Calmy Limestone, E₂, Gair, Carluke (HMUG L127; L129/1-5; L130/1, 5); Carboniferous Limestone, Lesmahagow (HMUG L4273/2). Staffordshire: Carboniferous Limestone, D₁, Narrowdale (GSM 84678). Yorkshire: Lower Carboniferous, C₂, Bolland (neotype BM B387); Elbolton Limestone Series, Tufa Beds, middle D₁ subzone, Elbolton Knoll, Cracoe (BC B139-156); Tufa-Cyrtina-Septosa Beds, middle D₁ subzone, same locality (BC B157); Tufa Beds, Stebden Knoll, Cracoe (BC B158-161); Carboniferous Limestone, Swinden, Grassington (IC 11130-11133); S₂ subzone, Stockdale Beck, Scaleber Bridge; Lower Carboniferous, Settle (BM B5709); Millstone Grit, Cayton Gill Beds, R₁, Fewston Bents Quarry, near Harrogate (BC B255-278); Cayton Gill Series, Cayton Gill, Markington (BM B34252); Millstone Grit, Pateley Bridge (BM B47673); Cayton Gill shell bed, near Darley (GSL 2829; 2830; 2914; 2915).

Schizophoria gibbera (Portlock) 1843

Plate 18, fig. 3; text-figs. 5-7

1843 *Atrypa* (*Porambonites*) *gibbera* Portlock, p. 460, pl. 38, fig. 1.

1844 *Orthis gibbera* (Portlock); M' Coy, p. 124, pl. 18, fig. 9.

1861 *Orthis resupinata* var. *gibbera* (Portlock); Davidson, p. 130, pl. 29, fig. 5.

1934 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, p. 55, pl. 4, fig. 4, *non* 1-3.

1941 *Schizophoria gibbera* (Portlock); Bond, p. 295, pl. 22, figs. A-D, H.

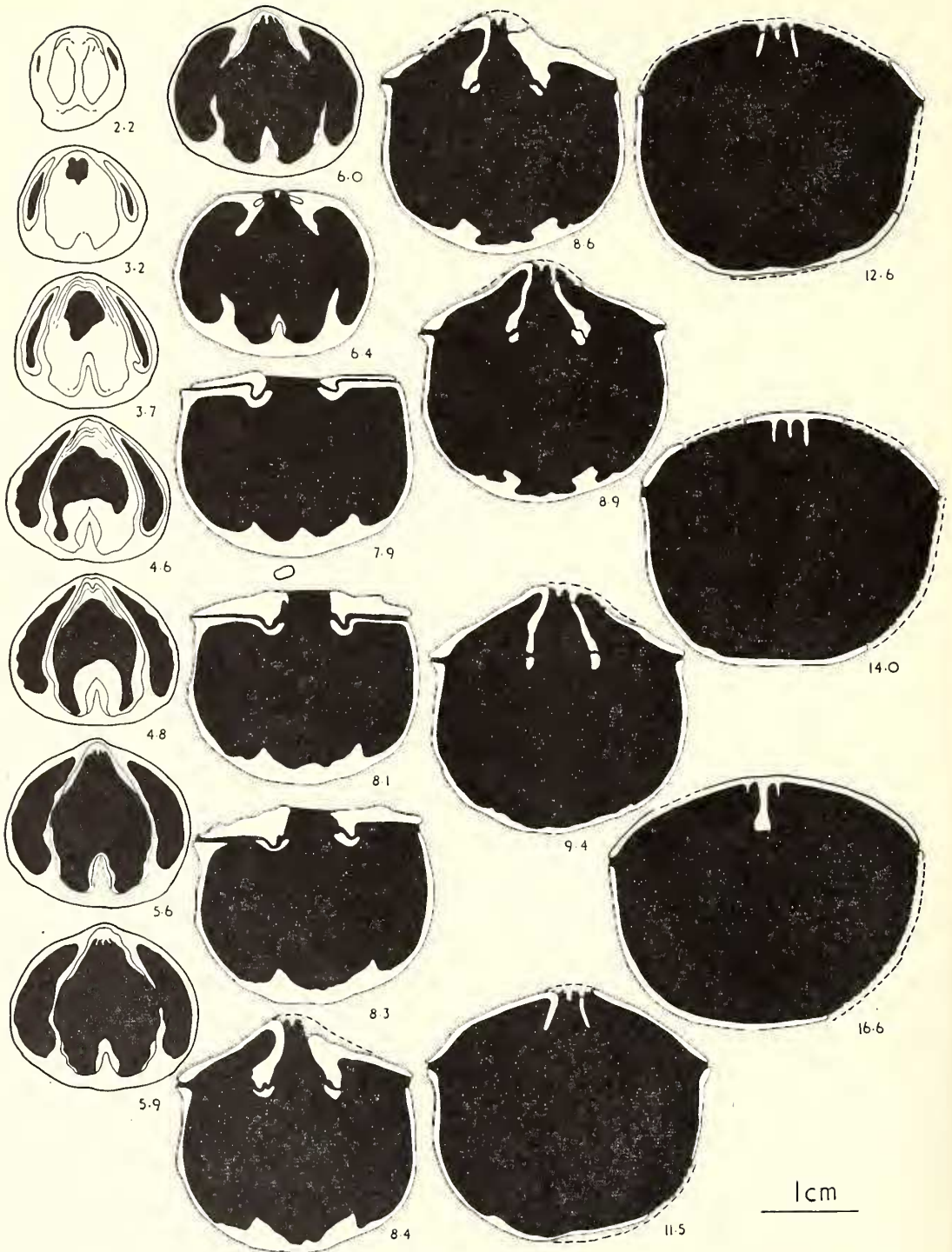
non 1923 *Schizophoria resupinata* var. *gibbera* (Portlock); Demanet, p. 121, pl. 5, fig. 2.

Type. The holotype is deposited in the Geological Survey Museum, GSM 70646.

Diagnosis. Medium to large, elliptical to rounded, deeper than long, strongly dorsibiconvex. Ventral sulcus absent. Dorsal concentric fold. Shell finely costellate, with scattered thickened costellae. Ventral muscle field very narrow, parallel-sided, strongly incised. Dorsal muscle field rectangular to elliptical, strongly incised, bounded posteriorly by curved brachiophore plates.

Description. Shell wider and deeper than long, with greatest width near mid-length. Low, ventral, concentric fold developed anteriorly, decreasing postero-laterally. Concentric dorsal fold developed posteriorly, disappearing laterally. Low, flat-topped, transverse dorsal fold occasionally developed. High, rounded anterior uniplication. Costellae fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered costellae thickened, irregularly spaced, 6 to 15 normal costellae apart. Growth rugae more prominent anteriorly.

Teeth compound, anteriorly parallel ventrally convergent dental lamellae (text-fig. 5, sections 8.3-9.4). Ventral muscle field (text-fig. 6) approximately one-half valve length, narrow, parallel-sided, strongly incised. Median septum narrow, rounded, increasing in



TEXT-FIG. 5. *Schizophoria gibbera* (Portlock). Transverse serial sections (GSI 21/4); C_{1-2} zones, Limerick; Length 26.7 mm., width 31.8 mm., depth 26.2 mm.

height and broadening anteriorly; becoming club-shaped anteriorly, and continuing for a short distance anterior of muscle field (text-fig. 5, sections 8.6–16.6). Two divergent *vascula media*. Genital markings developed postero-laterally (text-fig. 6).

Myophore small, compound, with central ridge bordered by two lateral ridges. Stubby brachiophores fused to slender, long, curved brachiophore plates (text-fig. 5, sections 3.2–6.4). Dental sockets oval, articulating with ventral teeth (text-fig. 5, sections 7.9–8.3). Dorsal muscle field (text-fig. 6) strongly incised, rectangular to elliptical, longer than wide, one-half to two-thirds valve length; anterior boundary ill-defined. Median septum broad, angular, first broadening, then narrowing and decreasing in height, and becoming subrounded anteriorly (text-fig. 5, sections 4.8–8.1). Genital markings developed postero-laterally.

Dimensions. External dimensions and dimensions of muscle fields of *S. gibbera* are as follows (in mm.):

	<i>Length</i>	<i>Width</i>	<i>Depth</i>	<i>Hinge-line (length)</i>
GSM 70646	31.1	34.6	31.2	—
BC B164	26.6	29.3	26.8	—
BM BB7350	29.0	35.6	33.9	25.2
BM BB7351	25.0	27.9	25.0	—
GSM 5758	24.0	26.3	25.6	18.2
GSI 21/4	24.4	30.5	26.0	23.9
21/4	26.7	31.8	26.2	22.3
21/4	29.4	37.7	29.3	—
SME 6577	27.5	31.8	31.0	—
TCD 1265	23.2	31.8	27.5	20.3

Ventral Muscle Field

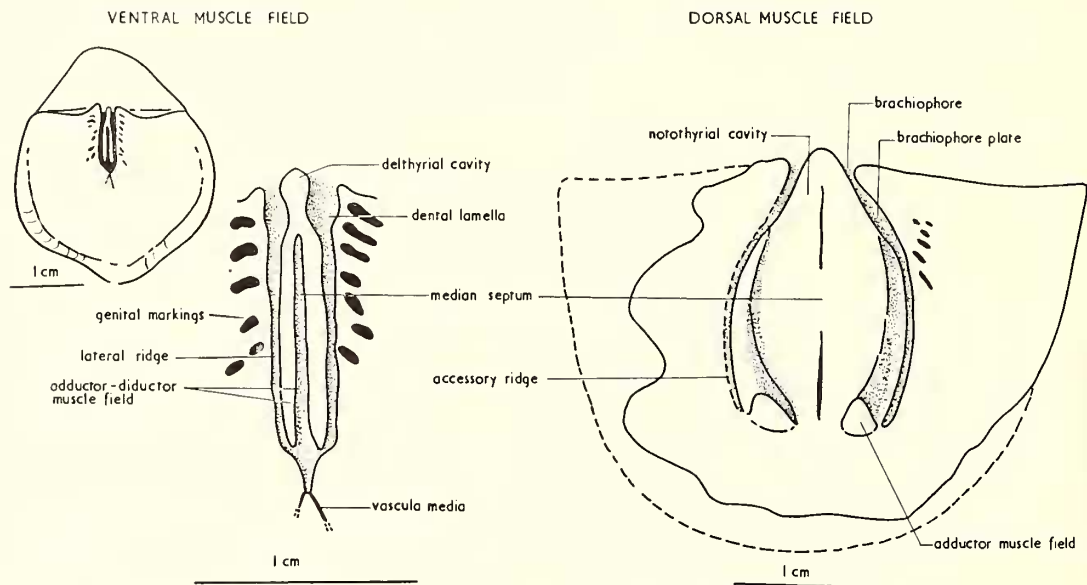
	<i>Length</i>	<i>Width</i>
GSM 5758	13.0	2.8

Dorsal Muscle Field

	<i>Length</i>	<i>Width</i>
BC B165	16.4	11.6
TCD 1270	13.8	11.3

Remarks. *S. gibbera* superficially resembles adult specimens of *S. linguata* (Quenstedt), in outline and costellation. Both species are strongly convex, have concentric folds, a rounded uniplication, and are finely costellate with scattered coarser costellae. But specific differences in size and outline are shown on text-fig. 7A. Internally, there are superficial similarities. Both have a narrow, parallel-sided ventral muscle field with a median septum extending beyond the anterior boundary, and a pair of divergent *vascula media*. *S. gibbera* has a wider muscle field in proportion to valve width, but it is shorter (one-half valve length) and the median septum and diductor muscle field are similar in width. The ventral muscle field of *S. linguata* is one-half to two-thirds valve length, with the median septum broadening anteriorly, and becoming wider than the diductor muscle field (text-fig. 7B). In the dorsal valve, both species have a rectangular to elliptical muscle field, bounded posteriorly by long, slender, curved brachiophore plates. *S. gibbera* has a more strongly incised muscle field, with strong accessory ridges continuous with the brachiophore plates, and a strong median septum (text-fig. 7B).

Schizophoria gibbera also superficially resembles adult forms of *S. woodi* Bond. Demanet (1934, pl. 5, figs. 1-3) figured *S. woodi* under *S. gibbera*. Both species are dorsibiconvex and finely costellate, but *S. gibbera* is more convex, and has a more inflated dorsal umbo. *S. gibbera* is more rounded in outline, and wider than long, while *S. woodi* may be as long as, or longer than, wide. There are other differences. *S. gibbera*



TEXT-FIG. 6. *Schizophoria gibbera* (Portlock). Ventral and dorsal muscle fields, based on specimens GSM 5758; TCD 1270. Ventral muscle field also enlarged.

has a fold on both valves, no ventral sulcus, and a deep, broad, rounded, anterior plication, in contrast to the generally smoother valve profiles or dorsal fold, angular ventral sulcus, and subangular plication of *S. woodi*.

Material. Ireland: Waulsortian, C₁₋₂ zones, Buttevant, Cork (TCD 1265, 1270); Carboniferous Limestone, C₂S₁, Little Island, Cork (GSM 5758); Carboniferous Limestone, C₂S₁-D₂, Tyrone (holotype GSM 70646). Lancashire: Lower Carboniferous, C₂, Bolland (BM BB7350, 7351); Worston Shale Group, C₂S₁ zone, Bellman Quarry, Clitheroe (BC B164, 165).

Schizophoria linguata (Quenstedt) 1871

Plate 18, figs. 4, 5; text-figs. 8-11

1871 *Orthis linguata* Quenstedt, p. 565, pl. 55, figs. 152-4.

1934 *Schizophoria resupinata* var. *palliata* Demanet, p. 58, pl. 4, figs. 7, 8.

1941 *Schizophoria palliata* Demanet; Bond, p. 297, pl. 22, fig. E, fig. 36.

non 1930 *Orthis* (*Schizophoria*) *linguata* Quenstedt; Paeckelmann, p. 175, pl. 9, fig. 15.

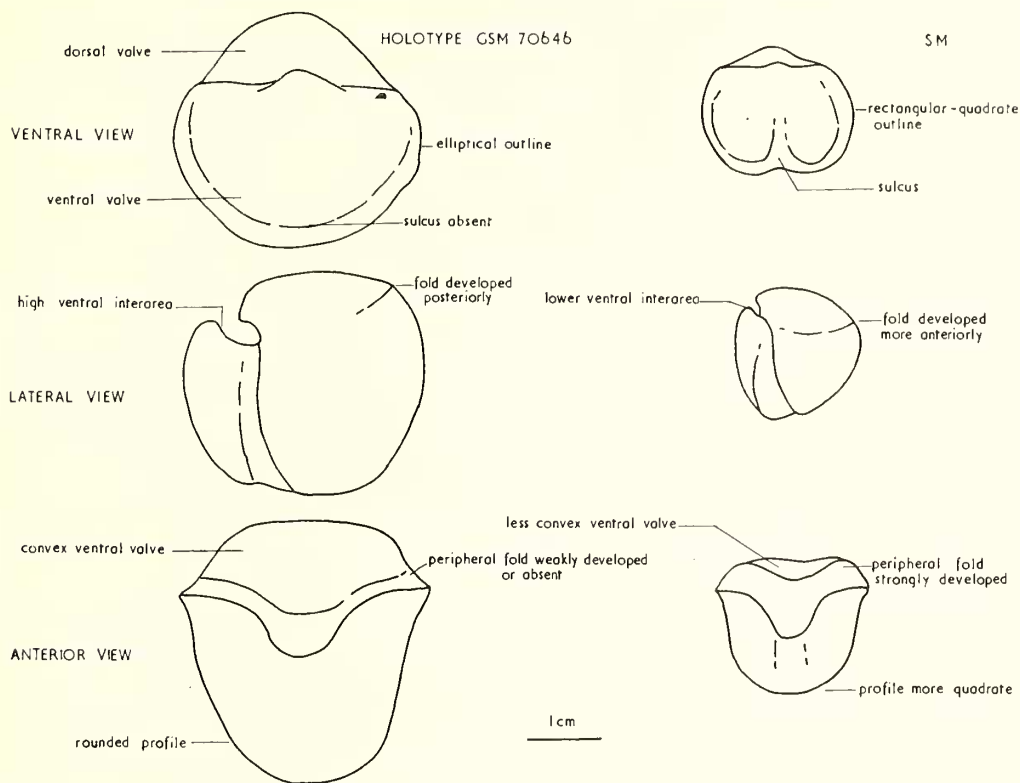
Types. Quenstedt's specimens are deposited in the Museum für Geologie und Paläontologie, Tübingen.

Diagnosis. Medium to small, rectangular to quadrate, with concentric ventral and dorsal folds. Great ontogenetic variation in dorsibiconvexity. Shell very finely costellate, with

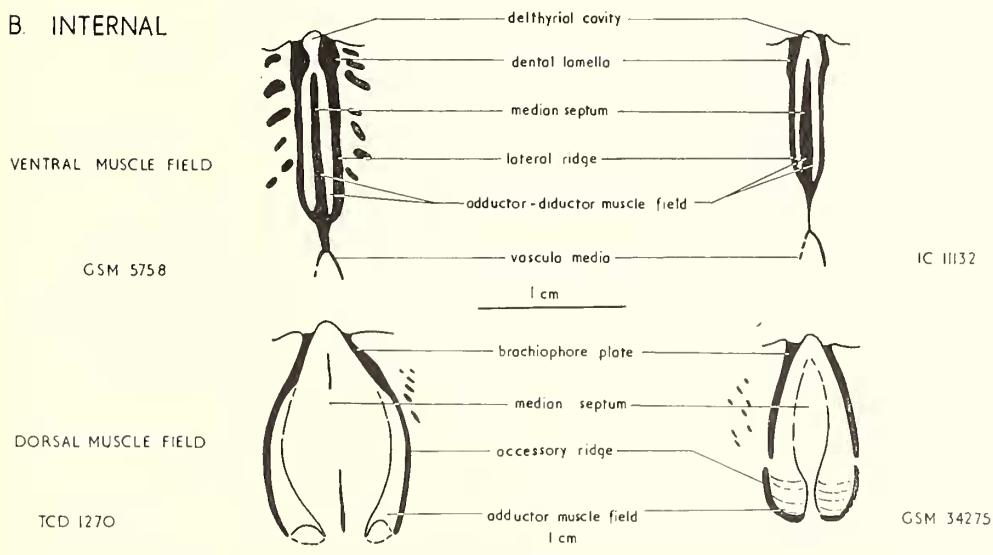
A. EXTERNAL

S. GIBBERA (PORTLOCK)

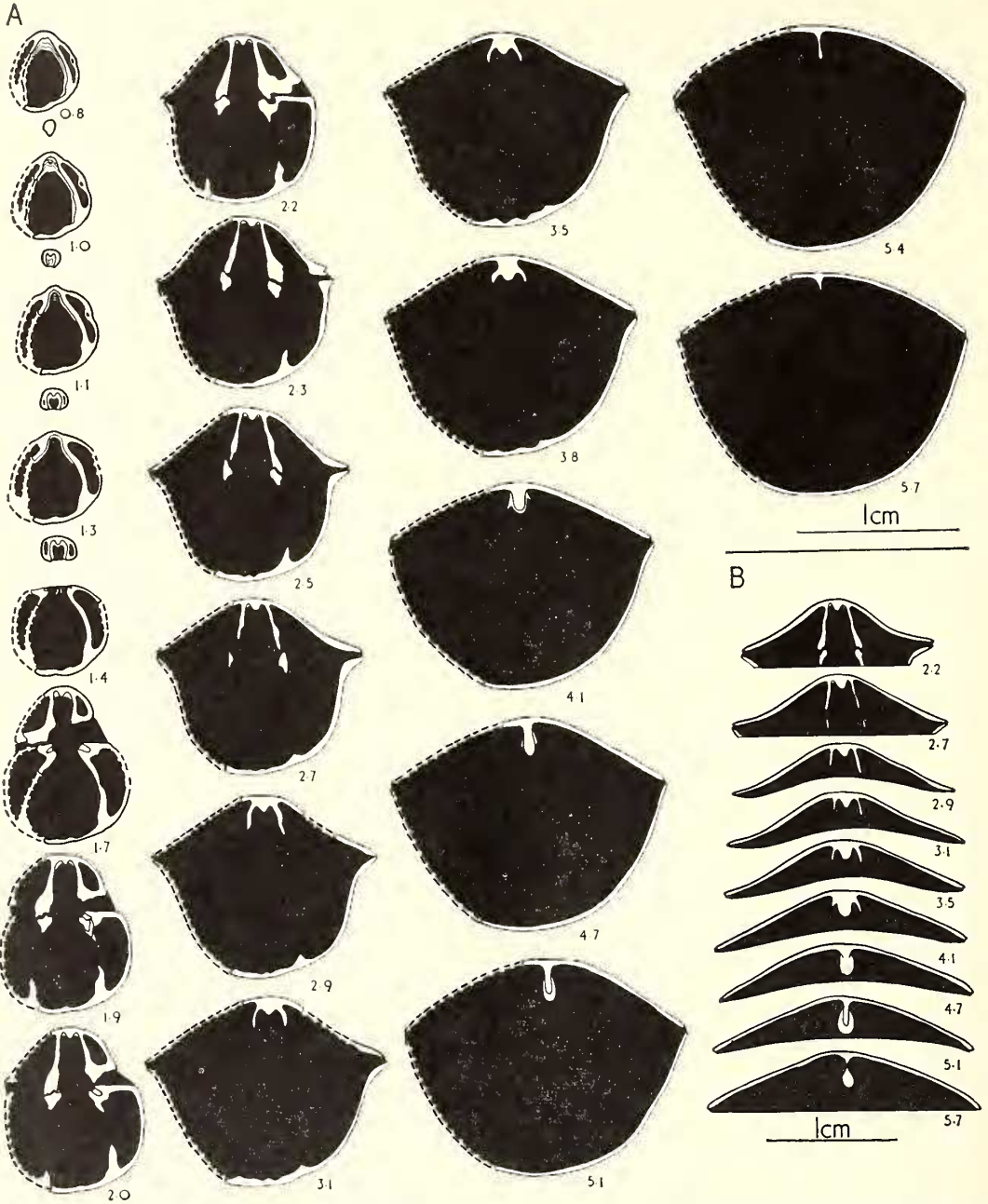
S. LINGUATA (QUENSTEDT)



B. INTERNAL



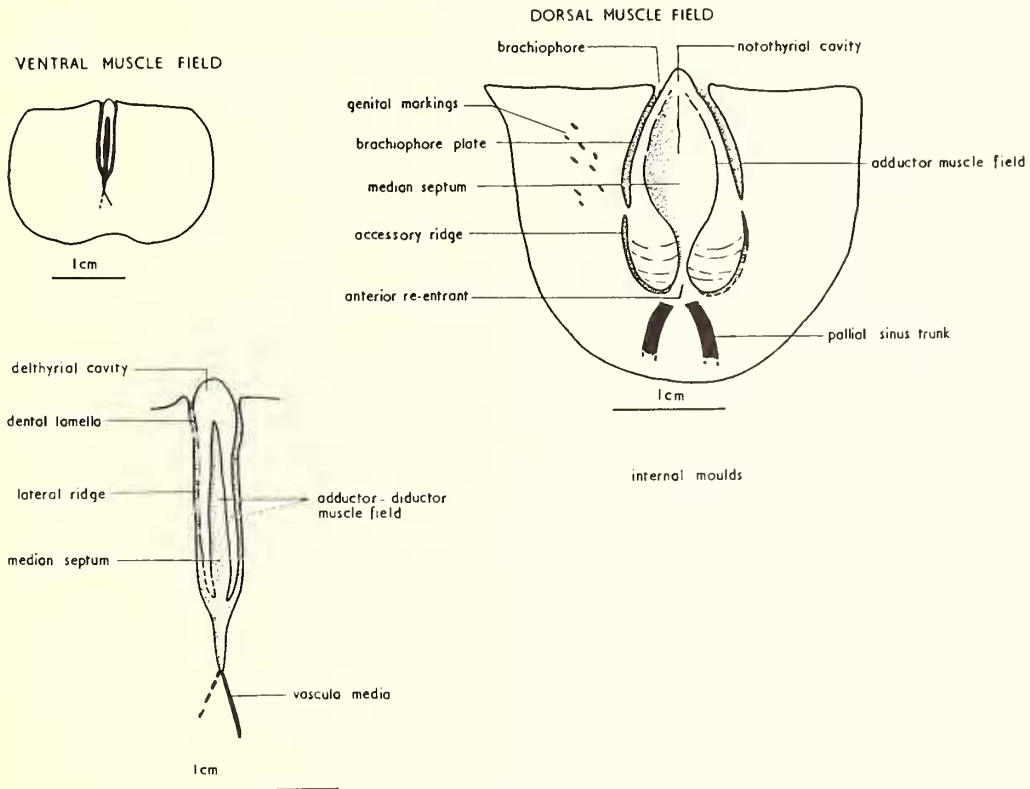
TEXT-FIG. 7. Specific differences between *Schizophoria gibbera* (Portlock) and *Schizophoria linguata* (Quenstedt).



TEXT-FIG. 8. *Schizophoria linguata* (Quenstedt). Transverse serial sections (A—SM D.22.B; B—SM D.22.B); D₁ zone, Craven, Yorkshire; A—length 14.1 mm., width 16.4 mm., depth 9.7 mm.; B—length 14.9 mm., width 18.8 mm., depth 14.4 mm.

scattered thicker costellae. Ventral muscle field strongly incised, very narrow, parallel-sided. Dorsal muscle field rectangular to elliptical, bounded posteriorly by curved brachiophore plates.

Description. Shell, biconvex to dorsibiconvex in young stages, dorsibiconvexity increasing with age, wider than long, with greatest width at mid-length. Ventral concentric fold,



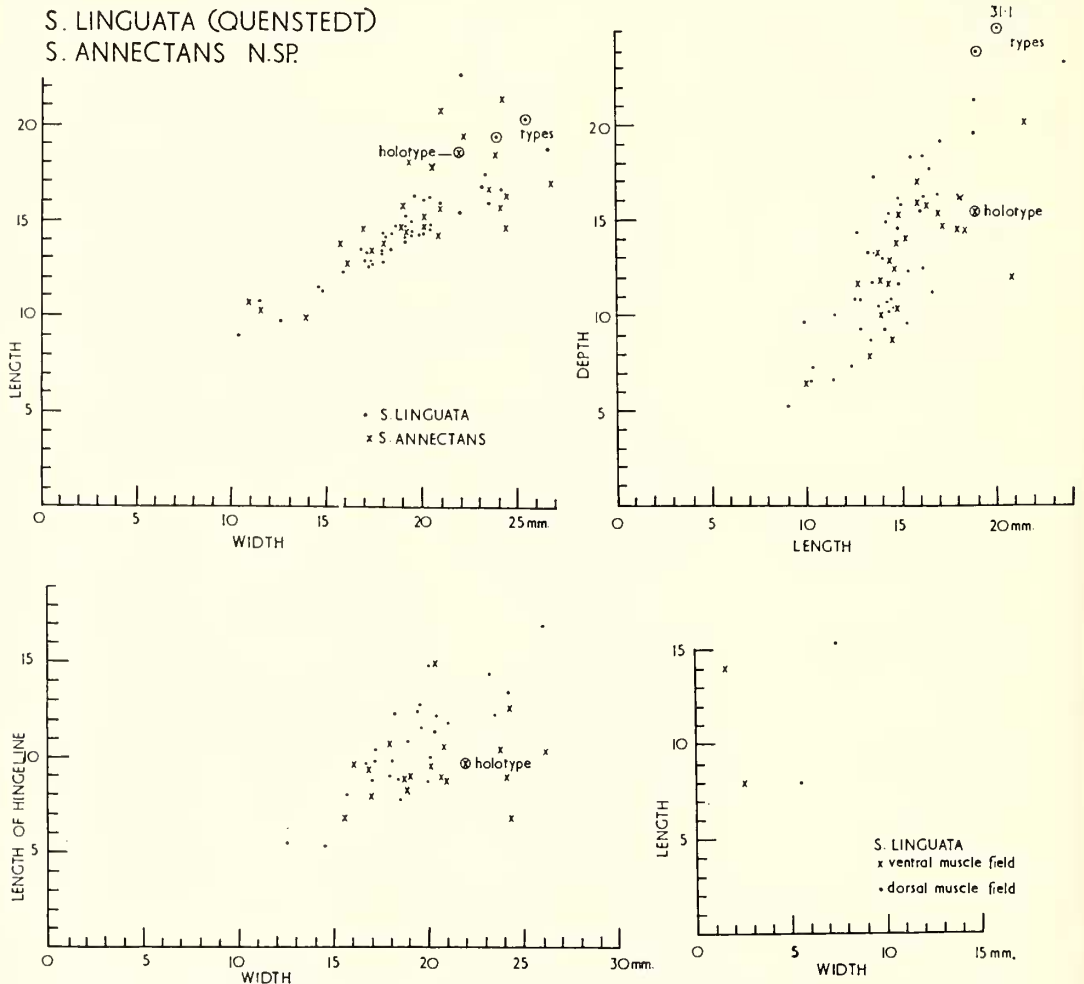
TEXT-FIG. 9. *Schizophoria linguata* (Quenstedt). Ventral and dorsal muscle fields, based upon specimens GSM 34295; IC 11134; SM D.22.B. Ventral muscle field also enlarged.

broken medially by sulcus. Dorsal concentric fold developed; low transverse fold occasionally developed anteriorly. High, broad, rounded anterior uniplication. Costellae very fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered coarser costellae. Rugae developed anteriorly and laterally.

Teeth compound, supported by anteriorly parallel and ventrally parallel to convergent dental lamellae (text-fig. 8A, sections 1.4-2.7). Ventral muscle field (text-fig. 9) one-half to two-thirds valve length, very narrow, parallel-sided, strongly incised. Median septum rounded, increasing in height and becoming subrounded anteriorly, then narrowing and decreasing in height, and extending for short distance beyond anterior of muscle field (text-fig. 8A, sections 1.1-5.7). Two divergent vascula media (text-fig. 9).

Myophore simple, or rudimentarily compound, with central ridge bordered by two

lateral ridges. Stubby brachiophores fused to slender, long, curved brachiophore plates (text-fig. 8A, sections 0.8–1.9). Dental sockets oval, articulating with ventral teeth (text-fig. 8A, sections 1.9–2.2). Dorsal muscle field (text-fig. 9) moderately incised, longitudinally rectangular to elliptical, one-half to two-thirds valve length. Accessory ridges



TEXT-FIG. 10. Dimensions of *Schizophoria linguata* (Quenstedt) and *Schizophoria annectans* sp. nov.

smoothly reflexed anteriorly to form shallow, subrounded re-entrant. Median septum broad, low, narrowing anteriorly (text-fig. 8A, sections 1.3–3.8). Two poorly preserved pallial sinus trunks originating from anterior re-entrant. Genital markings developed postero-laterally (text-fig. 9).

Dimensions. External dimensions are plotted on text-fig. 10. Dimensions of *S. annectans* sp. nov. have been added, to indicate its affinities with *S. linguata*.

Remarks. Quenstedt (1868–71) described and illustrated adult specimens under *Orthis linguata*.

Demagnet (1934) described two specimens under *S. resupinata* var. *palliat*a, but these were youthful forms, unlike the adult, strongly dorsibiconvex specimens of Quenstedt. *Schizophoria linguata* displays a great ontogenetic increase in dorsibiconvexity.

Bond (1941) illustrated this range in dorsibiconvexity. He did not list *S. linguata* in synonymy with *S. palliat*a, but stated that *S. linguata* cannot be considered conspecific with *S. palliat*a, since Demagnet (1934, p. 59) stated that *S. linguata* has only 5 costellae per mm. Although Bond gives 9 to 10 costellae per m., only 6 to 7 costellae have been measured in this study.

Orthis linguata and *Schizophoria palliat*a are thus considered to be synonymous, and *S. linguata* is used in priority over *S. palliat*a.

S. linguata shows close affinities with *S. annectans*. Youthful specimens have a comparable outline, convexity, anterior plication, and costellation (text-fig. 11). Both are rectangular to elliptical, biconvex, and finely costellate with scattered thickened costellae. But *S. annectans* has a narrower anterior plication. Adult specimens of the two species are similarly alike, but *S. annectans* has a more elliptical outline, is less strongly dorsibiconvex, and lacks the characteristic concentric folds (text-fig. 11).

Internally there are also close similarities in muscle fields, dental lamellae, brachio-phores and brachio-phore plates, but *S. annectans* has a more prominent, rounded to anteriorly flat-topped ventral median septum. Although there is variation in the strength of the median septum of *S. linguata* (text-fig. 8B), it is less prominent than that of *S. annectans*.

Adult, strongly dorsibiconvex forms of *S. linguata* resemble *S. gibbera* (Portlock). Similarities and differences are dealt with under the latter species.

Youthful biconvex, rectangular to elliptical forms of *S. linguata* superficially resemble *S. resupinata* (Martin), but *S. linguata* has finer costellae. Internally, the narrower, parallel-sided ventral muscle field, longitudinally rectangular to elliptical dorsal muscle field, and curved brachio-phore plates of *S. linguata* contrast with the broader, flabellate ventral muscle field, transversely elliptical dorsal muscle field, and divergent brachio-phore plates of *S. resupinata*.

Material. Belgium, Dinant: Tournaisian, Tn3bR, Dréhance (IRSN 3200). Caldbeck, Cumberland: Lower Carboniferous, S₂-D₁ (BM B75348). Derbyshire: Viséan, D₁ zone, Treak Cliff, Castleton (BM B40846); Lower Carboniferous, Dovedale (GSM 34274, 5, 34277, 34279); Lower Carboniferous, C₁₋₂, Thorpe Cloud (BM B4108). Staffordshire: Lower Carboniferous, D₁, Narrowdale (GSM 39/29, 84675-7), Wetton (BM B13190, 34459); Lower Carboniferous, D₂ subzone, Narrowdale (BM B49065-8). Yorkshire: Carboniferous Limestone, C₂, Bolland (BM B26199); Lower Carboniferous, Settle (SM E6773); Wharfedale (BM B34453).

Schizophoria annectans sp. nov.

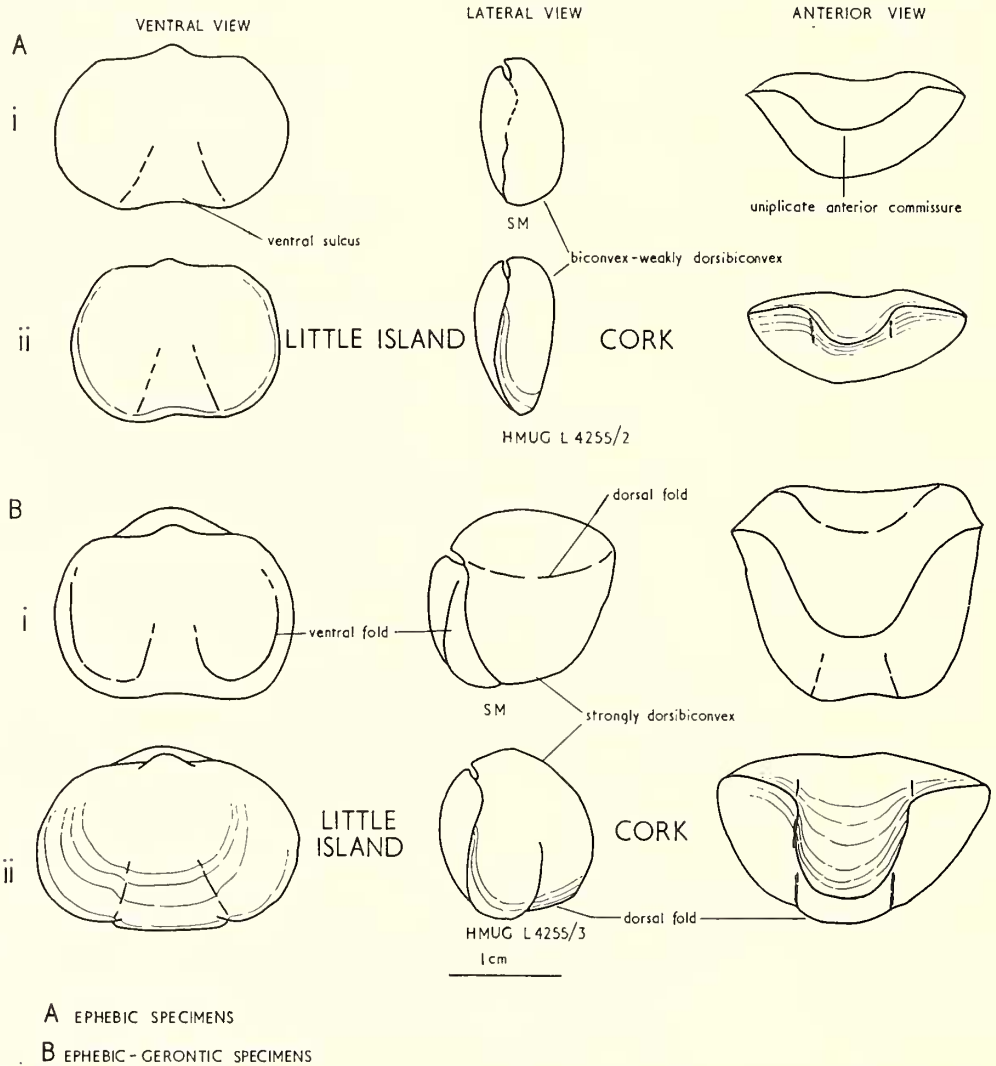
Plate 18, fig. 6; text-figs. 10, 12

1930 *Orthis* (*Schizophoria*) *linguata* Quenstedt; Paeckelmann, p. 175, pl. 9, fig. 15.

Type. The holotype is deposited in the British Museum (Natural History), B40126.

Diagnosis. Medium to small, rectangular to elliptical. Shell very finely costellate, with scattered coarser costellae, and rugate. Ventral muscle field strongly incised, narrow, parallel-sided, with broad, rounded median septum. Curved brachio-phore plates.

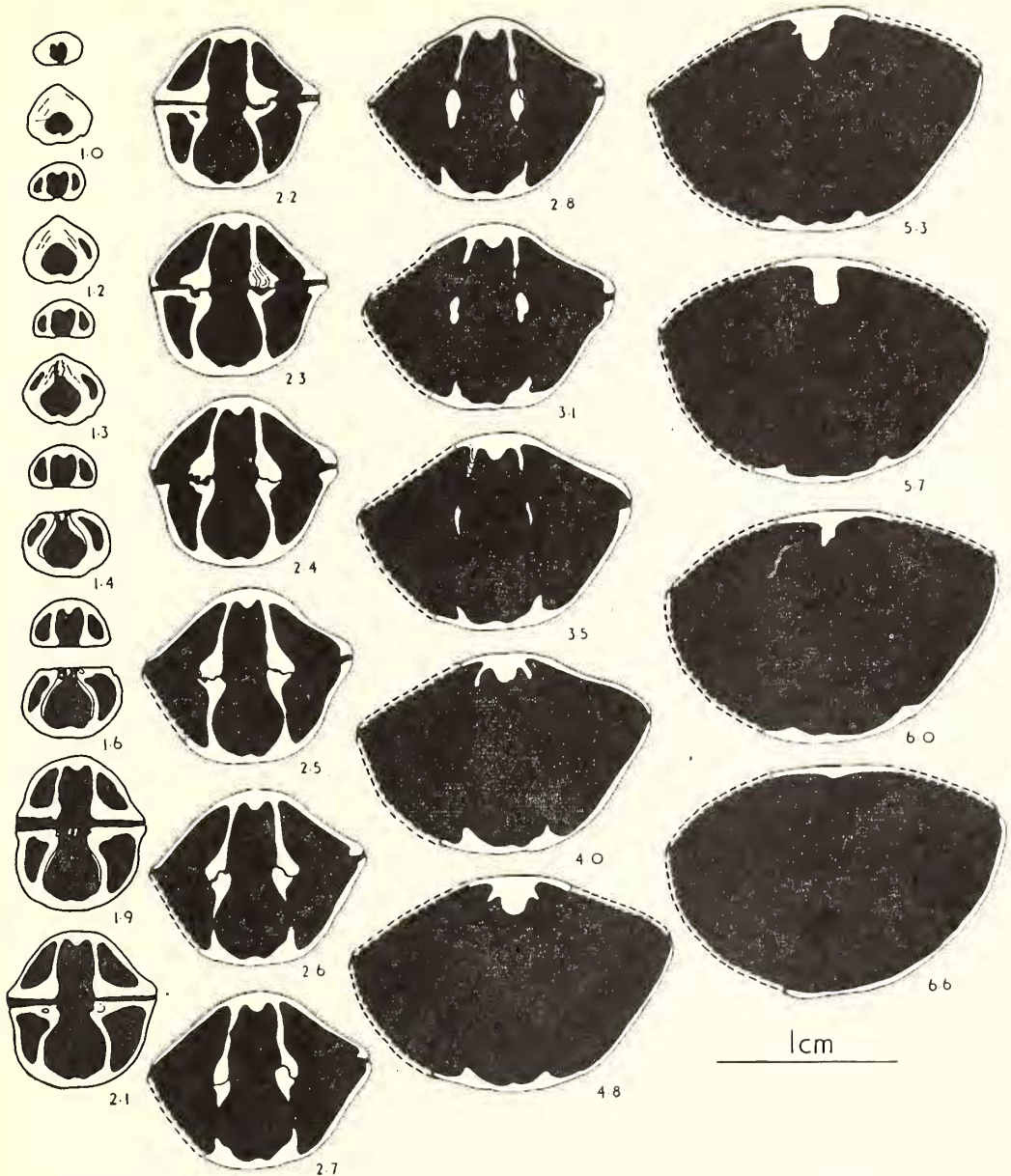
Description. Shell biconvex to moderately dorsibiconvex, wider than long, with greatest width at mid-length. Ventral sulcus originating anterior of umbo, broadening and deepening anteriorly; well-defined laterally in older specimens. Dorsal fold occasionally



TEXT-FIG. 11. Comparison of *Schizophoria linguata* (Quenstedt) (A (i) ephebic shell; B (i) ephebic-gerontic shell) and *S. annectans* sp. nov. (A (ii) ephebic shell; B (ii) ephebic-gerontic shell).

developed anteriorly. High, broad, rounded anterior plication. Costellae very fine, 6 costellae in 1 mm. at 10 mm. from beaks. Scattered coarser costellae. Prominent rugae, concentrated anteriorly and laterally.

Teeth compound, supported by anteriorly parallel and ventrally parallel to convergent dental lamellae (text-fig. 12, sections 1.2-2.8). Articulation supplemented by interlocking ends of dental lamellae and brachiophores (text-fig. 12, sections 2.7-2.8). Ventral



TEXT-FIG. 12. *Schizophoria annectans* sp. nov. Transverse serial sections (HMUG L4255/1); C₂S₁ zone, Little Island, Cork; length 12.8 mm., width 19.8 mm., depth 14.3 mm.

muscle field approximately one-half valve length, narrow, parallel-sided, strongly incised. Median septum rounded, broadening and increasing in height anteriorly, and extending for short distance anterior of muscle field (text-fig. 12, sections 1.0-6.6).

Myophore simple, or rudimentarily compound, with central ridge, bordered by two lateral ridges. Stubby brachiophores fused to strong, long, curved brachiophore plates

(text-fig. 12, sections 1.4–2.7). Dental sockets oval, articulating with ventral teeth. Dorsal muscle field moderately to strongly incised, longer than wide, approximately one-half valve length. Median septum broad, low, rounded, increasing, then decreasing in height anteriorly (text-fig. 12, sections 1.2–6.0).

Dimensions. External dimensions are plotted on text-fig. 10.

Remarks. Internal moulds of *S. annectans* are not available, but in transverse serial sections, the muscle fields have a similar general outline to those of *S. linguata*.

In the British Isles, *S. annectans* is apparently limited to Little Island, Cork and the Valley of the Maine, Ireland, apart from three specimens from the Craven area of Yorkshire.

Although possessing close affinities with *S. linguata*, hence the derivation of *annectans*—linking or connecting form, *S. annectans* does show external and internal differences. These have been described under *S. linguata*.

Paeckelmann (1930, p. 175, pl. 9, fig. 15) described and illustrated a specimen from the Lower Carboniferous of Germany under *Orthis (Schizophoria) linguata* (Quenstedt). This resembles *S. annectans* in outline, fine costellae and prominent rugae, anterior uniplication, and short anterior dorsal fold.

Material. Ireland: Carboniferous Limestone, C₂S₁, Little Island, Cork (BM B40126, 68454; GSI 75/3; GSM 5730, 5732; HMUG L1841/2, 5, 4255/1–5; SME 6875); Valley of the Maine (GSM 3758, 3759); Yorkshire: Lower Carboniferous, D₁, Craven (SM).

Schizophoria resupinata (Martin) 1809

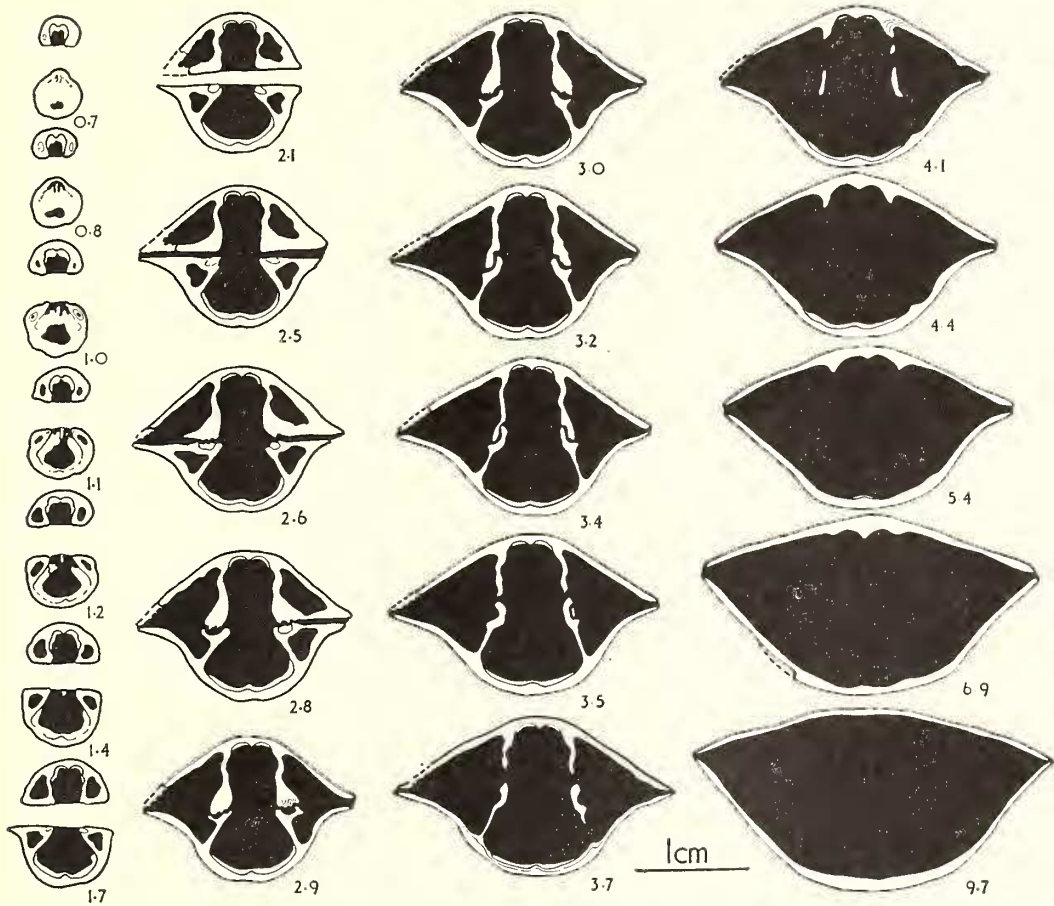
Plate 18, fig. 7; text-figs. 13–15

- 1777 *Anomites* Schröter, p. 352, pl. 5, fig. 2.
 1809 *Conchyolithus anomites (resupinatus)* Martin, pl. 49, figs. 13, 14.
 1823 *Terebratula resupinata* (Martin); Sowerby, pl. 325.
 1836 *Spirifer resupinata* (Martin); Phillips, p. 220, pl. 11, fig. 1.
 1842–4 *Orthis resupinata* (Martin); de Koninck, p. 226, pl. 13, figs. 9, 10.
 1853 *Orthis resupinata* (Martin); Davidson, pl. 7, fig. 135.
 1861 *Orthis resupinata* (Martin); Davidson, p. 130, pl. 29, figs. 1–3; pl. 30, figs. 1–5.
 1871 *Orthis resupinata* (Martin); Quenstedt, p. 563, pl. 55, figs. 146–9 (148—var. *lata?*).
 1873 *Orthis resupinata* (Martin); de Koninck, p. 47, pl. 2, fig. 5b.
 1877 *Orthis resupinata* (Martin); de Koninck, p. 214, pl. 10, fig. 9.
 1923 *Schizophoria resupinata* (Martin); Demanet, p. 119, pl. 5, fig. 1.
 1934 *Schizophoria resupinata* (Martin); Demanet, p. 47, text-fig. 9, pl. 3, figs. 1–5.
 1938 *Schizophoria elboltonensis* George and Ponsford, text-figs. 6, 7.
 1938 *Schizophoria nuda* George and Ponsford, p. 224, pl. 5, figs. 1–5, text-figs. 1–5.
 1941 *Schizophoria resupinata* (Martin); Bond, p. 289, pl. 21, figs. A–C.
 1942 *Schizophoria resupinata* (Martin); Délépine, p. 59, pl. 6, figs. 16, 17; 1946, p. 27, pl. 6, figs. 16, 17.
 1950 *Schizophoria resupinata* (Martin); Termier and Termier, pl. 71, figs. 27–30; pl. 73, figs. 1–7, 10, 11; pl. 77, figs. 8, 9.
 1954 *Schizophoria resupinata* (Martin); Parkinson, p. 368, figs. 1, 2a–e.
 1957 *Schizophoria* cf. *S. resupinata* (Martin); Campbell, p. 48, pl. 12, figs. 1–5; text-figs. 3–5.
 1958 *Schizophoria verulamensis* Cvančara, p. 856, pl. 109, figs. 14–16; pl. 110, figs. 1–5.
 1934 *Schizophoria resupinata* var. *dorsosinuata* Demanet, pl. 3, figs. 14, 15.
 1938 *Schizophoria* cf. *dorsosinuata* Demanet; George and Ponsford, text-figs. 10–14.
 1941 *S. resupinata* var. *dorsosinuata* Demanet; Bond, p. 289, figs. 33, 34.

1923 *Schizophoria resupinata* var. *lata* Demanet, p. 122, pl. 5, fig. 4: 1934, pl. 3, figs. 6-8.

1941 *S. resupinata* var. *lata* Demanet; Bond, p. 290, figs. 33, 34.

1934 *Schizophoria resupinata* var. *gigantea* Demanet, p. 60, pl. 4, figs. 12, 13.



TEXT-FIG. 13. *Schizophoria resupinata* (Martin). Transverse serial sections (IC 11138); D₁ zone, Swinden, Yorkshire; Length 23.0 mm., width 30.0 mm., depth 16.0 mm.

1861 *Orthis resupinata* (Martin); Davidson, pl. 29, fig. 3.

1934 *Schizophoria resupinata* var. *pinguis* Demanet, p. 59, pl. 4, figs. 9-11.

1938 *Schizophoria pinguis* Demanet; George and Ponsford, text-figs. 8, 9.

1941 *S. resupinata* var. *pinguis* Demanet; Bond, p. 290.

1934 *Schizophoria resupinata* var. *rotundata* Demanet, p. 17, pl. 3, figs. 9-13.

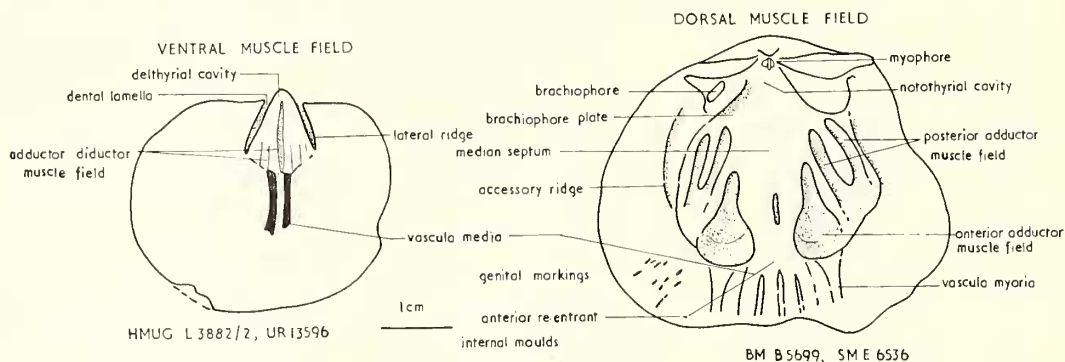
Types. Martin's holotype (1809) is lost. The neotype, chosen by George and Ponsford (1938) and figured by Bond (1941) is deposited in the British Museum (Natural History), BB2420.

Diagnosis. Medium to large, rectangular to elliptical. Ventral muscle field moderately incised, flabellate. Slender divergent brachiophore plates.

Description. Shell ventribiconvex to moderately dorsibiconvex, wider than long, with

greatest width at mid-length. Ventral sulcus generally ill-defined, except for broad, shallow depression developed anteriorly. Dorsal sulcus frequently developed. Anterior commissure varying from rectimarginate to broadly uniplicate, unisulcate or weakly sulcinate. Costellae fine, 4 to 5 in 1 mm. at 10 mm. from beaks. Scattered coarser costellae, with spine bases developed anteriorly.

Teeth compound, supported by anteriorly divergent, ventrally subparallel, dental lamellae (text-fig. 13, sections 1.1–3.5). Articulation supplemented by interlocking ends of dental lamellae and brachiophores (text-fig. 13, sections 3.2–3.5). Ventral muscle field (text-fig. 14) less than one-half valve length, flabellate, moderately incised; anterior boundary often ill-defined. Median septum narrow, subrounded, generally broadening and increasing in height slightly anteriorly (text-fig. 13, sections 0.7–6.9). Two parallel vascula media (text-fig. 14).



TEXT-FIG. 14. *Schizophoria resupinata* (Martin). Ventral and dorsal muscle fields, based on specimens BM B5699; HMUG L3882/2; SM E6536; UR13596.

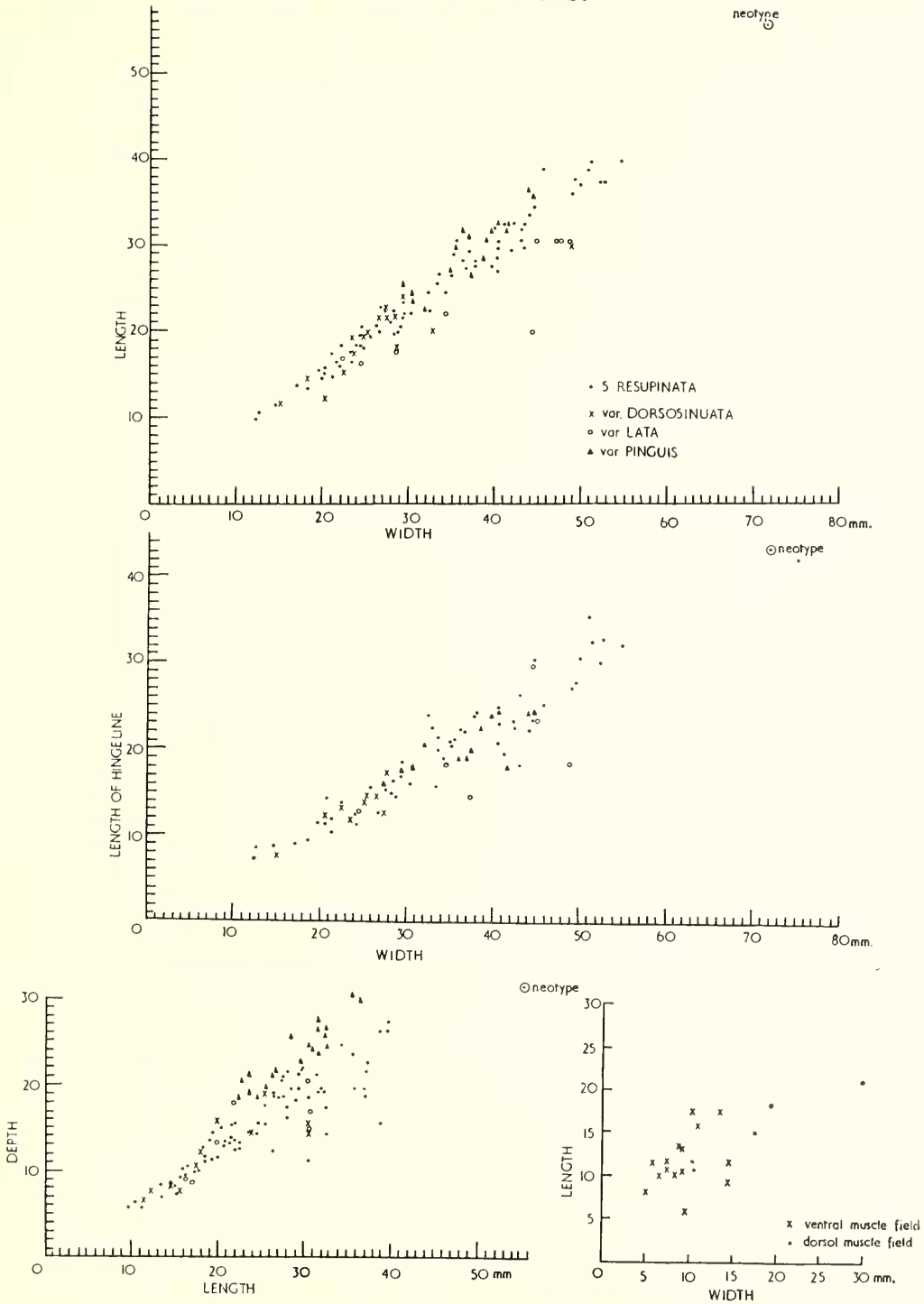
Myophore large, average width 2.5 mm., with central ridge bordered by two or four lateral ridges. Stubby brachiophores fused to slender, divergent brachiophore plates (text-fig. 13, sections 1.4–3.7). Deep dental sockets articulating with ventral teeth (text-fig. 13, sections 2.6–3.0). Dorsal muscle field (text-fig. 14) moderately incised, transversely elliptical, one-third to one-half valve length. Accessory ridges smoothly reflexed to form rounded anterior re-entrant. Median septum subangular, broadening anteriorly (text-fig. 13, sections 1.2–6.9). Four vascula media originating from anterior re-entrant, two vascula myaria originating from ends of anterior adductor muscle scars. Genital markings developed postero-laterally (text-fig. 14).

Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 15.

Remarks. The neotype chosen by George and Ponsford closely resembles Martin's lost holotype in outline, convexity and dorsal sulcus, but is larger. *S. resupinata* varies in size, but only one other specimen of similar proportions has been plotted on text-fig. 15. Although resembling the holotype, it was an unfortunate choice of neotype, since it is so much larger than an average specimen.

Variation. Although *S. resupinata* is a long ranging species (K–D zones), there is little change in morphology from early to late forms. Slight variations in convexity, outline, anterior plication, and development of a dorsal sulcus and thickened costellae and spine

S. RESUPINATA (MARTIN) & VARIETIES



TEXT-FIG. 15. Dimensions of *Schizophoria resupinata* (Martin).

bases occur within specimens from one horizon and between specimens from different horizons.

Some specimens from Treak Cliff, Derbyshire, differ from the characteristic form of *S. resupinata* in outline, convexity, and costellation. They are more elliptical in outline, biconvex to dorsibiconvex, and have coarser costellae, 3 to 4 in 1 mm. Differences in relative convexity of the valves is correlated with internal variations in the relative lengths of dental lamellae and brachiophore plates. Apart from a broader ventral median septum, the two forms are similar internally.

Varieties. Demanet (1923, 1934) established five varieties of *S. resupinata*, *dorsosinuata*, *gigantea*, *lata*, *pinguis*, and *rotundata*.

Schizophoria resupinata var. *dorsosinuata* is characterized by medium size, quadrate to rectangular outline, a dorsal sulcus, fine costellae, and prominent rugae. The variant resembles *S. resupinata*, except that the dorsal sulcus is more consistently developed, and the rugae more prominent. Internally there is close similarity, except that the ventral muscle field of *dorsosinuata* is more incised, and the median septum broader.

There is a tendency for some specimens to become much wider than long. They resemble the variant *lata* in width, but have the characteristic dorsal sulcus and rugae of *dorsosinuata*.

The variant *gigantea* is recognized by its large size, semi-elliptical outline, and strongly convex dorsal valve. Internally, the ventral muscle field resembles that of *S. resupinata*.

Demanet established var. *lata* on its length : width ratio, elliptical outline and broad anterior ventral sulcus. The ventral muscle field of *lata* is comparable with that of *S. resupinata*.

The variant *pinguis* was diagnosed on its inflated outline. It is characterized by large size, a rounded, strongly dorsibiconvex outline, and prominent rugae. Internally, it closely resembles *S. resupinata*, except that the muscle fields are more incised.

Two specimens from the British Museum, BB40159 and B54136 are more transversely elongate forms of *pinguis*, resembling *lata* in length : width ratio.

Specimens of *S. resupinata* range from weakly dorsibiconvex to more strongly dorsibiconvex forms. These represent Parkinson's (1954) thin and thick forms. Parkinson attempted to show an evolutionary trend from thin to thick forms collected from C and D zones of the Lower Carboniferous. He believed that thick forms are characteristic of the D zone, but although thin forms are characteristic of the C zone, they also occur in the D zone. The variant *pinguis* appears to represent the acme of inflation, and is restricted to the D zone (Parkinson 1954). However, specimen BM B386 was collected from the C₁ subzone of Bolland, and BM B54136 from the C₁₋₂ subzones of Thorpe Cloud, Derbyshire.

Schizophoria resupinata var. *rotundata* was established on small size, rounded outline, even convexity and lack of ventral sulcus. No specimens other than Demanet's type have been recognized.

All variants of *S. resupinata* are rare, and generally recur at different horizons, although most have been examined from the D zone. Out of approximately several hundred specimens of *S. resupinata*, the following numbers of variant specimens have been examined: *dorsosinuata*—22; *gigantea*—4; *lata*—10; *pinguis*—17; *rotundata*—1. Externally they are recognized by their varietal features, but internally they closely

resemble *S. resupinata*, except for slight details of muscle fields. A sporadic appearance of a few variant specimens possibly suggests that they merely represent a few mutant forms showing extreme variation. Many intermediate stages are seen trending towards extreme forms. Combinations of variation are seen in inflated and transversely elongate forms of var. *pinguis*, and elongate forms of *dorsosinuata*.

Extreme variation may have been induced by environmental conditions. Bond (1941, p. 209) stated that *dorsosinuata* may be the result of unfavourable conditions causing stunting and development of rugae, after a period of normal growth. But rugate and non-rugate specimens of *S. resupinata* occur together. *Gigantea* could represent a few large individuals which flourished under favourable conditions. The inflated *pinguis* occurs alongside less convex forms of *S. resupinata*.

The varietal names are descriptive of the several variation trends, but synonymies and descriptions of variants have been included under *S. resupinata* to emphasize their close relationship to the species, and as merely representing extreme individual variation.

Comparisons of species. *Schizophoria elboltonensis* George and Ponsford is distinguished externally from *S. resupinata* by its more quadrate outline. Serial sections by George and Ponsford (1938, text-fig. 7) illustrated stubby brachiophores and short, stout brachiophore plates, in contrast to the more tapered brachiophores and longer, more slender brachiophore plates of *S. resupinata*. Since *S. elboltonensis* differs only in respect of its quadrate outline, brachiophores and brachiophore plates, and no additional specimens have been examined, the species has been listed under *S. resupinata*.

In 1938 George and Ponsford also described *S. nuda*. This is a large form, characterized by an elliptical outline with greatest width near the hinge-line, and strongly incised muscle fields. The ventral muscle field of *S. nuda*, its flabellate outline, median septum, and even variation in muscle field outline, clearly conform to that of *S. resupinata*. In the dorsal muscle field, the outline, digitate posterior adductors, variations in median septum and pallial sinus trunks of *S. nuda* also closely resemble those of *S. resupinata*. The only distinction is relative incision, and incision is in part correlated with age. These large specimens could represent old forms. *Schizophoria nuda* accordingly has been listed in synonymy with *S. resupinata*.

Youthful specimens of *S. resupinata* superficially resemble young forms of *S. woodi* Bond in their rectangular to elliptical outline. But *S. resupinata* has a rectimarginate to rounded uniplicate, unisulcate or sulcate anterior commissure, coarser costellae, and a lack of rugae, in contrast to the rectimarginate to angular uniplication, finer costellae, and more prominent rugae of *S. woodi*. Adult specimens are also distinguished by their outline and convexity. *S. resupinata* is wider than long, and moderately dorsibiconvex, while *S. woodi* may also be as long as wide, or longer than wide, and strongly dorsibiconvex. Internal differences can be seen by comparing text-figs. 13 and 16.

Material. Belgium, Dinant: Viséan, Furfooz (IRSN 1301); Tournaisian, Tn 3, Tournai (var. *dorsosinuata*) (IRSN 3440, 5496, 8261); same stratigraphical level, Furfooz (var. *dorsosinuata*) (IRSN 3200); Tournaisian, Tn3bR, Weve (var. *dorsosinuata*) (IRSN 4447); same level, Dréhance (var. *lata*) (IRSN 3200); Tournaisian, Lez-Fontain (var. *lata*) (IRSN 8760); Tournaisian, Furfooz (var. *pinguis*) (IRSN 1301); Tournaisian, Tn3bR, Vère Chateau (var. *pinguis*) (IRSN 4447). Avon Gorge: Tournaisian, Z₁₋₂ subzones (BC B166). Derbyshire: *Dielasma* Bed, D₁ subzone, Treak Cliff, Castleton (BC B167-9); B₂ subzone, Treak Cliff (BM B14879); Lower Carboniferous, D₂, Park Hill, Longnor (GSM 84670, 84681, 84683); Lower Carboniferous, C₁₋₂, Thorpe Cloud (var. *pinguis*) (BM B54136); Viséan,

D₁ zone, Eldon Hill (var. *pinguis*) (BM BB40159, 40161, 40167, 40169, 40171, 40172; HMUG L5333/1). Isle of Man (Castletown): Poyllvaish Limestone, P_{1a} subzone (D₂), near Poyll Vaaish (BC B170–85); Poyllvaish Limestone, near Poyll Vaaish (var. *gigantea*) (BC B186); same level and locality (var. *lata*) (BC B187); Lower Carboniferous, D_{2a}, Poyll Vaaish (var. *pinguis*), (HMUG L4256; SME 6487). Ireland: Viséan, Carrick syncline (HMUG L3882/2); Viséan, D₁ zone, Curkeen Hill, Dublin (TCD 3019, 3042, 3044, 3048); Waulsortian, C_{1–2} zones, Ballylin, Limerick (UR 13590, 13596); Carboniferous Limestone, C_{1–2}, Ballydoole, Limerick (var. *dorsosinuata*) (GSI 3/4). Lancashire: Worston Shale Group, C₂S₁ zone, Clitheroe (BC B189–94; GSM 3691, 3709, 84666; SME 13607); Carboniferous Limestone, C₂, Bolland (var. *pinguis*) (BM B386). Yorkshire: Carboniferous Limestone, C₂, Bolland (neotype BM BB2420, B384, B8328); Elbolton Limestone Series, *Cyrtina septosa* D₁ subzone, Elbolton Knoll, Cracoe (BC B195); Tufa-*Cyrtina septosa* Beds, D₁ subzone, Elbolton Knoll, Cracoe (BC B196–205); Viséan, D₁ subzone, Elbolton, Cracoe (var. *lata*) (BM BB8149, BS 4027); same level and locality (var. *pinguis*), (BM B54146; IC 11135); S₂ reef limestones, Stockdale Beck, Scaleber, Settle (var. *pinguis*) (BC B207).

Schizophoria woodi Bond 1941

Plate 18, fig. 8; text-figs. 16–19

1934 *Schizophoria resupinata* var. *gibbera* Demanet, pl. 4, figs. 1–3, non 4.

1941 *Schizophoria woodi* Bond, p. 299, pl. 22, figs. F, G; text-fig. 37.

1950 *Schizophoria resupinata* (Martin); Termier and Termier, pl. 71, fig. 31.

1952 *Schizophoria resupinata* (Martin); Wright, text-fig. 5 (3).

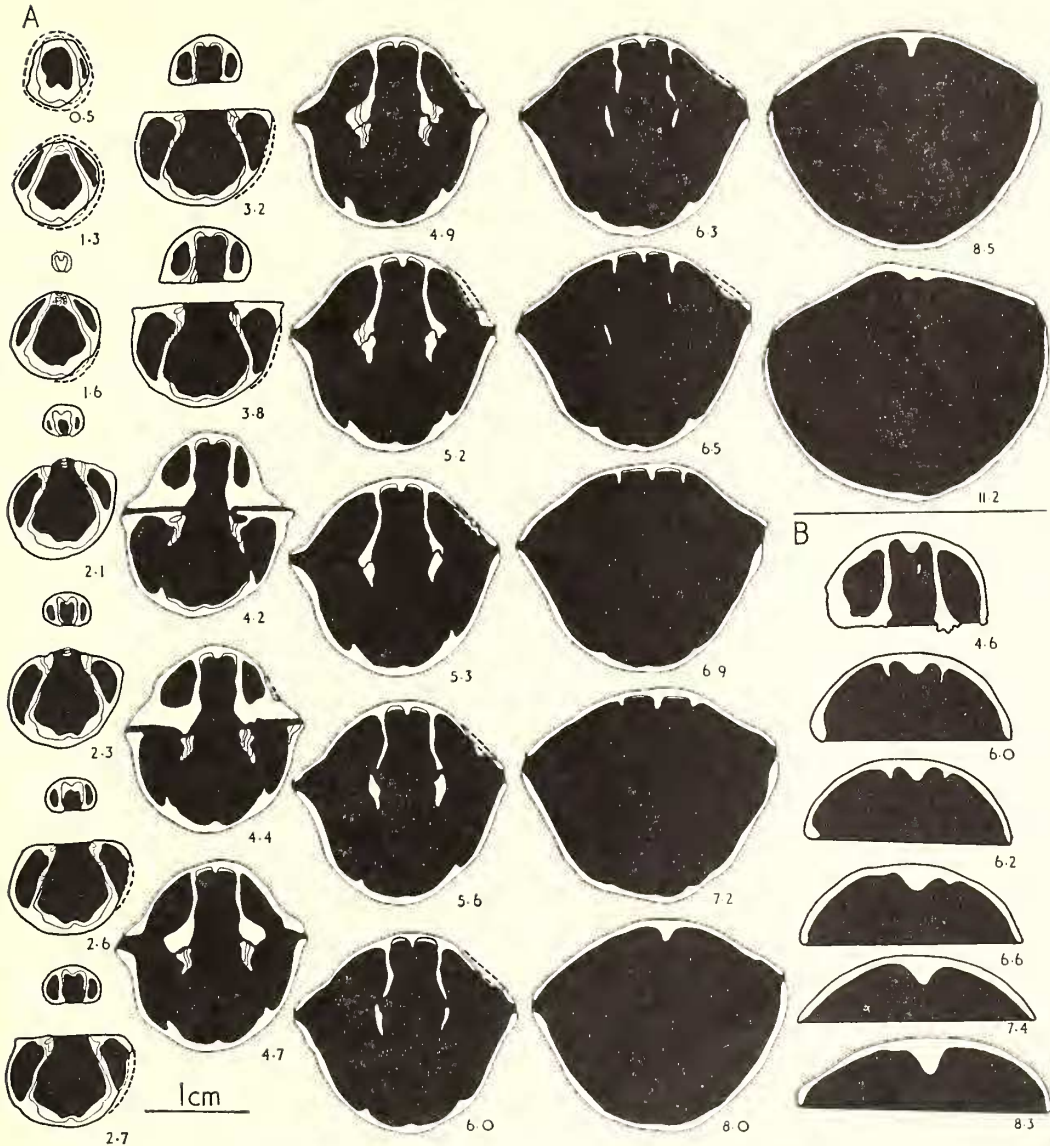
Type. The holotype is deposited in the British Museum (Natural History) BB8152.

Diagnosis. Small to large, rounded to elliptical, generally strongly dorsibiconvex, with narrow, groove-like ventral sulcus, and subangular uniplicate anterior commissure. Shell finely costellate. Ventral muscle field flabellate, strongly incised. Slender, curved brachiophore plates.

Description. Shell biconvex to strongly dorsibiconvex, with greatest width at mid-length. Ventral sulcus angular, originating half way along valve, broadening and deepening anteriorly. Narrow dorsal fold frequently developed anteriorly. Broad, subangular anterior uniplication. Costellae fine, 6 to 7 in 1 mm. at 10 mm. from beaks. Scattered thickened costellae. Prominent growth rugae.

Teeth compound, supported by anteriorly divergent, ventrally subparallel to convergent dental lamellae (text-fig. 16A, sections 2.1–6.3). Ventral muscle field (text-fig. 17) one-third to one-half valve length, flabellate, strongly incised. Deep, subrounded anterior re-entrant. Median septum narrow, rounded, broadening and increasing in height anteriorly (text-fig. 16A, sections 1.6–11.2). Two parallel vascula media (text-fig. 17).

Myophore compound, average width 1.5 mm., with central ridge bordered by two lateral ridges. Stubby brachiophores fused to slender, curved brachiophore plates (text-fig. 16A, sections 2.1–4.7). Deep dental sockets articulating with ventral teeth (text-fig. 16A, sections 4.2–4.4). Dorsal muscle field (text-fig. 17) moderately incised, flabellate, longer than wide, one-half valve length. Accessory ridges smoothly reflexed to form shallow subangular re-entrant. Median septum low, subrounded, slightly increasing in width and height anteriorly (text-fig. 16A, sections 2.1–8.0). Two vascula media originating from anterior re-entrant, two vascula myaria originating antero-laterally (text-fig. 17).

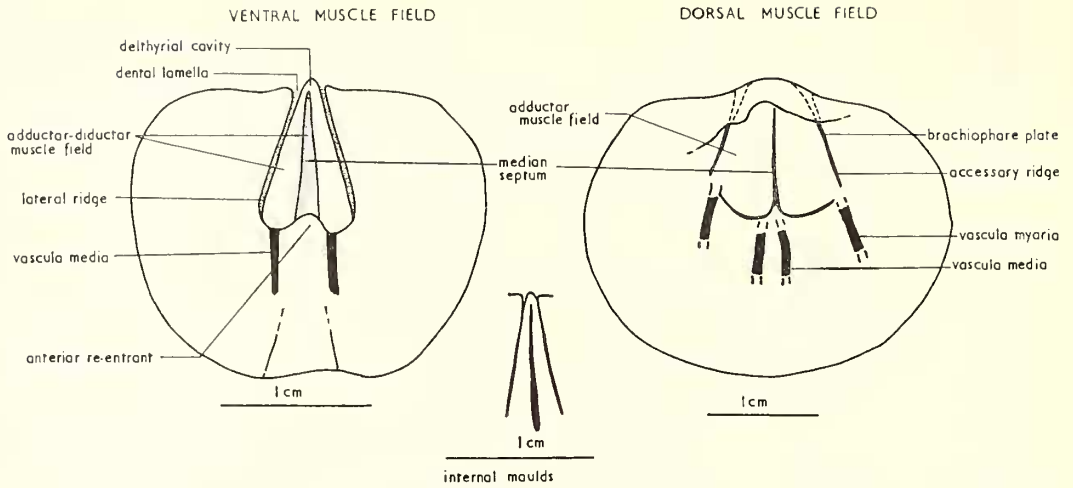


TEXT-FIG. 16. *Schizophoria woodi* Bond. Transverse serial sections (A—BC B248; B—BM B54120); D₂ zone, Isle of Man; A—length 26.1 mm., width 27.1 mm., depth 22.5 mm., B—length 25.7 mm., width 28.0 mm., depth 22.0 mm.

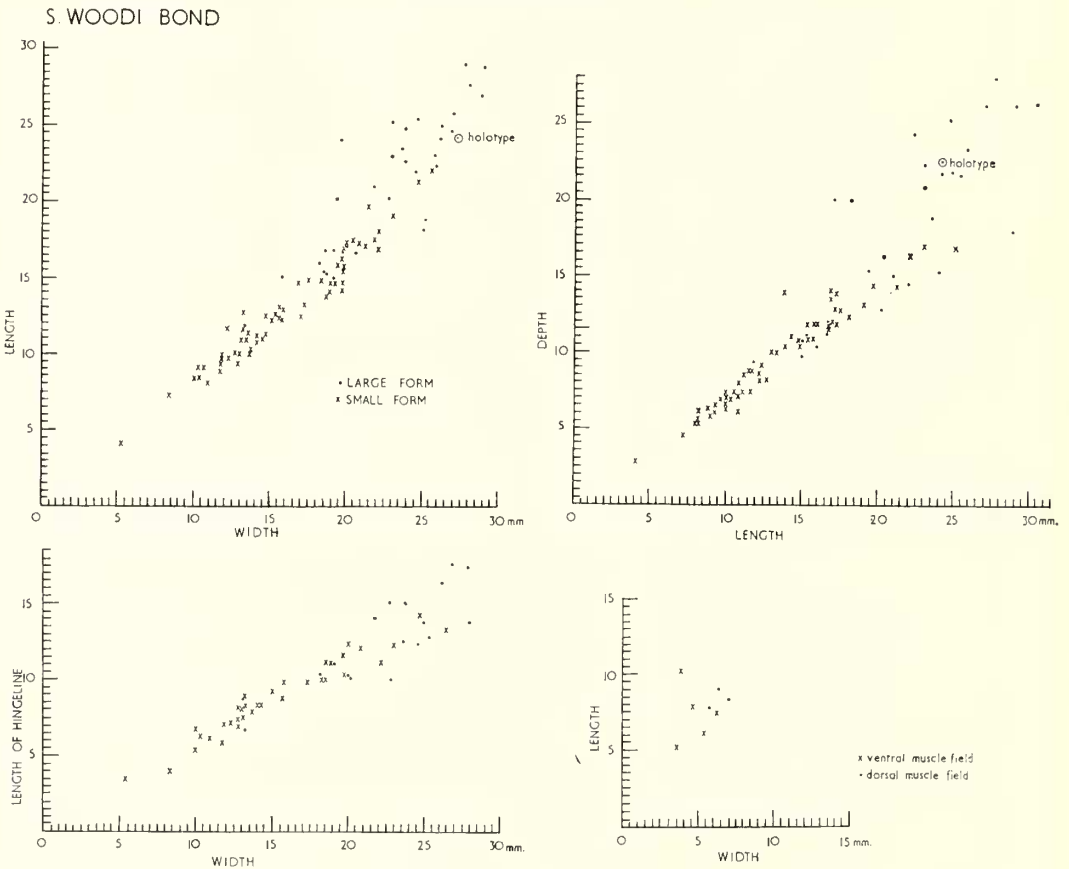
Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 18. Some smaller forms of *S. woodi* from Cracoe, Ireland and Treak Cliff have been plotted separately.

Remarks. Bond (1941, p. 299, text-fig. 37) illustrated variations in shell outline. Similar trends shown by Belgian specimens are illustrated on text-fig. 19.

Specimens assigned to *S. woodi* from Treak Cliff, Derbyshire and Swinden and Elbolton Knolls, Yorkshire, do not generally attain the same size and dorsibiconvexity



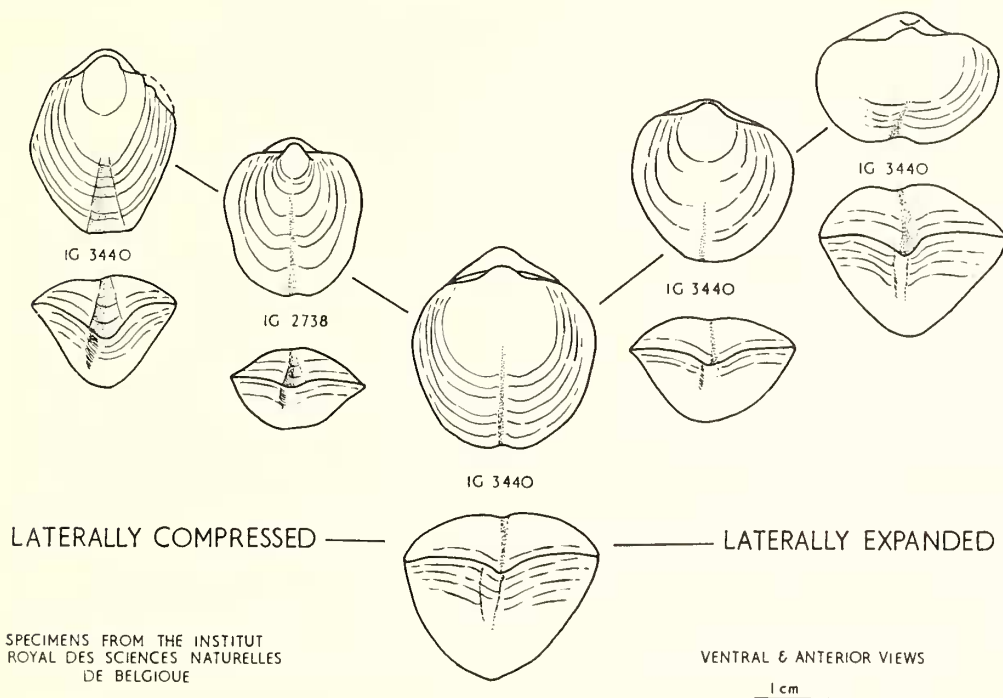
TEXT-FIG. 17. *Schizophoria woodi* Bond. Ventral and dorsal muscle fields, based on specimens BC B239, 250-2; BM BB39953.



TEXT-FIG. 18. Dimensions of *Schizophoria woodi* Bond.

as those from Craven and the Isle of Man. However, external and internal characters of the two forms are very similar.

Small, biconvex forms of *S. woodi*, especially from Elbolton and Swinden Knolls, and Treak Cliff, superficially resemble *S. connivens* (Phillips) in size, tumid outline, and prominent rugae. But *S. woodi* has fine costellae, less prominent rugae, and an angular-uniplicate anterior commissure, in contrast to the coarse costellae, thick rugae, and



TEXT-FIG. 19. External variation in *Schizophoria woodi* Bond.

quadrate-uniplicate or biplicate anterior commissure of *S. connivens*. Internally they are quite distinct (cf. text-figs. 16 and 1).

S. woodi superficially resembles *S. gibbera* (Portlock) in dorsibiconvexity and costellation. Although strongly dorsibiconvex and finely costellate, *S. woodi* has slightly coarser costellae and has rugae, and is less strongly dorsibiconvex. In other characters the two species are readily distinguishable (text-fig. 4).

Strongly dorsibiconvex individuals of *S. woodi* also superficially resemble comparable forms of *S. linguata* (Quenstedt) in outline and costellation. Both are strongly dorsibiconvex and finely costellate, but *S. woodi* is more rounded in outline, and has a narrower, more angular ventral sulcus and anterior plication, in contrast to the quadrate to rectangular outline, and rounded sulcus and plication of *S. linguata*. Internally the two species are distinct (text-figs. 16 and 8). Youthful specimens of the two species are generally distinct. *S. woodi* is more rounded in outline, more convex, and has a sub-angular anterior plication, in contrast to the rectangular to elliptical outline, and rounded plication of *S. linguata*.

Material. Belgium, Visé: Viséan (BM B13197/1, 6, 9; HMUG L1152/1, 2; IRSN 2737, 3440). Derbyshire: *Dielasma* Bed, D₁ subzone, Treak Cliff, Castleton (BC B208-36; BM BB39846, 39852, 39857, 39883, 39885, 39886, 39903, 39906, 39913, 39925, 39926, 39942, 39953); Avonian reef limestones, Treak Cliff (HMUG L5323/5, 9, 14, 44, 45, 63, 68, 70, 84, 87, 95, 123-5, 128). Ireland: Viséan, D₁ subzone, County Meath (TCD M2647b, 27125b). Isle of Man (Castletown): Poyllvaish Limestone, Upper Reef Knoll Limestone, P_{1a} (D₂) subzone, Ghaw Gortagh, near Poyll Vaish (BC B237-52); Lower Carboniferous (BM B54118-21). Yorkshire: Avonian reef limestones, Elbolton Knoll, Cracoe (HMUG L5321/7); Lower Carboniferous, D₁, Craven (BM BB8152—holotype); D₁ zone, Wedber Knoll, Malham (HMUG L3674/2; IC 11136; SM E11,128, 11,129).

PHYLOGENY

The postulated phylogeny of Carboniferous species of *Schizophoria* is shown on text-fig. 20. This chart is based solely on the available material, and could conceivably represent only a part of the true picture of descent.

The phylogeny of Devonian species has previously been described (Pocock, 1966).

The relationship of species has been based externally on outline and costellation, and internally on muscle field patterns and form of the brachiophore plates, correlated with stratigraphical distribution. These features are illustrated on text-figs. 20, 21.

Four main lines of development are recognized in the Carboniferous. The line of development represented by *S. connivens* consists of small to medium-sized, coarsely costellate, rugate forms, with divergent brachiophore plates, and an elliptical to weakly flabellate ventral muscle field.

The line represented by *S. resupinata* and its varieties is characterized by larger forms, with finer costellae, divergent brachiophore plates, and a flabellate ventral muscle field.

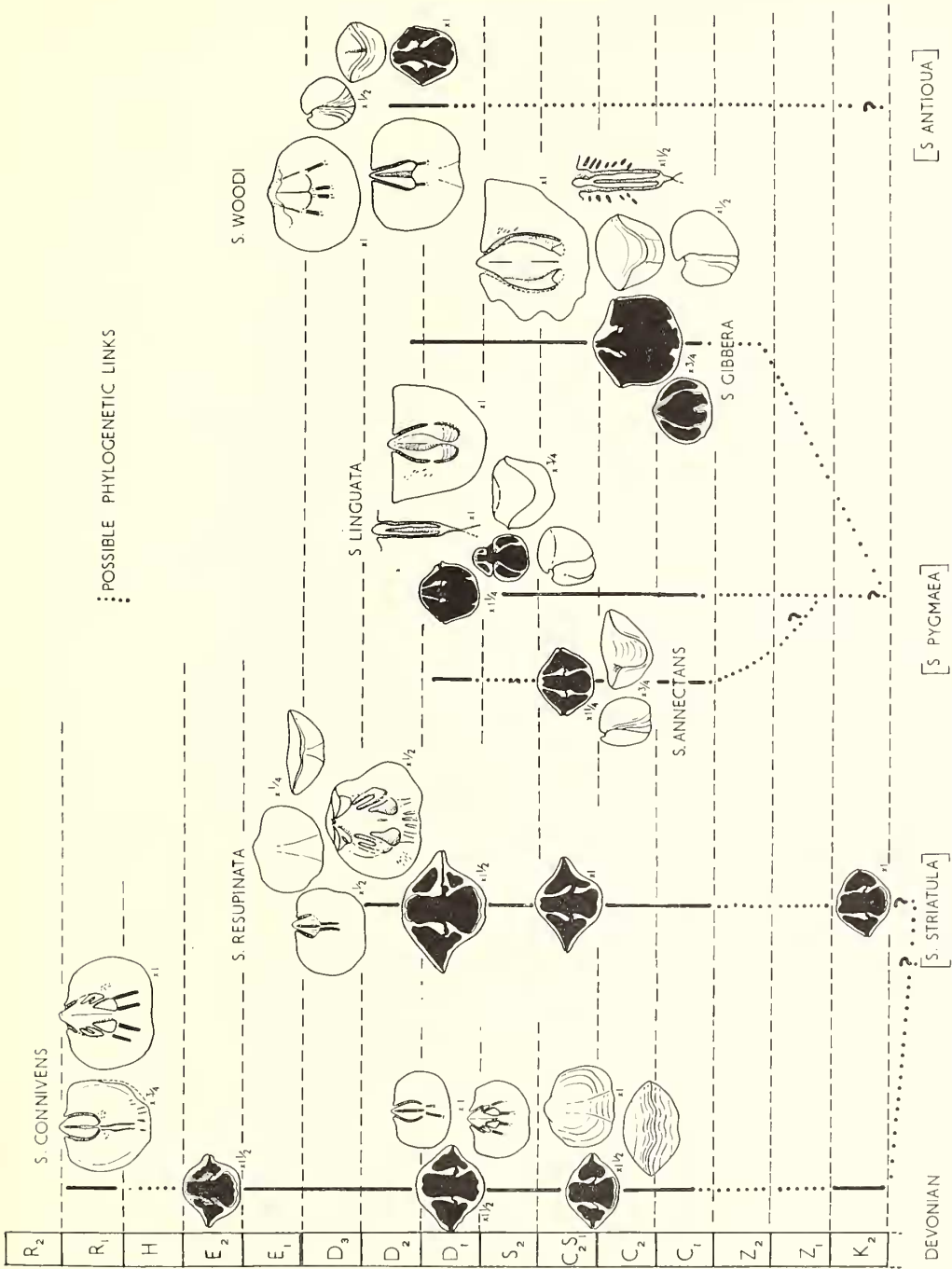
S. gibbera, *S. linguata*, and *S. annectans* represent a line composed of three branches, characterized by greater dorsibiconvexity, very fine ornament, a narrow, parallel-sided ventral muscle field, a rectangular to elliptical dorsal muscle field, and curved brachiophore plates.

S. woodi is the fourth line of development, and is similarly a strongly dorsibiconvex form with fine costellae, and curved brachiophore plates. But *S. woodi* has a flabellate ventral muscle field.

S. resupinata (K-D zones) was probably derived from the *S. striatula* line of development in the Devonian, based on general outline and muscle fields. The varieties of *S. resupinata* are shown as sporadic offshoots, representing extreme variation at different levels.

S. connivens (K zone—R₁ stage) has hereby been derived as an offshoot from *S. resupinata*, possibly in late Devonian or early Carboniferous. Although distinct from *S. resupinata*, there are some resemblances in the dorsal muscle field and brachiophore plates.

Derivation of the *gibbera-linguata-annectans* line (C-D zones) is difficult to postulate. Although *S. provulvaria* and *S. antiqua* of the Devonian have curved brachiophore plates, they have different external outline and muscle fields. The strongly dorsibiconvex forms, with narrow, parallel-sided ventral muscle fields of the Carboniferous are not represented by any closely comparable forms studied in the Devonian. Although *S. gibbera*, *S. linguata*, and *S. annectans* have been derived from the *S. provulvaria-S. pygmaea* line on text-fig.



TEXT-FIG. 20. Postulated phylogeny of *Schizophoria* from the Carboniferous of western Europe.